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Neotropical palm-inflorescence feeding moths (Lepidoptera: Batrachedridae, Blastobasidae, Cosmopterigidae, Gelechiidae, Pyralidae, Tineidae): a review of the literature and new records from Trinidad, West Indies

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Abstract. The insects associated with the inflorescences of palms (Arecaceae) and their roles as pollinators, pests and scavengers are not well known compared to foliage-feeders and trunk borers, especially in the Neotropical Region. A literature review of the Lepidoptera associated with palm inflorescences in the Neotropical Region is provided. In a preliminary survey of Lepidoptera associated with palm inflorescences in Trinidad (Trinidad and Tobago), more than one thousand moths of 12 species were reared from six of the 14 palm species sampled. Of the moths reared, three could not be identified beyond family, three could be identified only to genus, and the remaining six were identified to species. These six comprise two species that feed on flowers of *Cocos nucifera* and *Roystonea oleracea* (viz. *Atheloca bondari*, *Batrachedra nuciferae*) and four that are polyphagous, widespread detritivores (*Xystrologa nigrivitta*, *Anatrachyntis rileyi*, *Erechthias minuscula*, *Phidotricha erigens*). *Anatrachyntis rileyi* and *E. minuscula* are thought to be introduced moth species, while the others are indigenous. Biological observations are presented on the moths reared.

Keywords: *Anatrachyntis rileyi*, *Atheloca bondari*, *Batrachedra nuciferae*, *Erechthias minuscula*, *Holcocera* sp., *Neodavisia* sp., *Phidotricha erigens*, *Xystrologa nigrivitta*, Arecaceae, coconut.

INTRODUCTION

The insects associated with palms (Arecaceae), especially *Cocos nucifera* (coconut), have been relatively well documented (Lepesme, 1947; Lever, 1979; Howard *et al.*, 2001), but those associated specifically with the inflorescences and their roles as pollinators, pests and scavengers are less well known. Traditionally, palms were thought to be wind pollinated, but it has become clear in recent decades that insect pollination does occur

and may well be the norm rather than the exception (Moore, 2001). The floral ecology is variable among species (Henderson, 1986). Some have hermaphrodite flowers, others are monoecious (containing flowers of both sexes) in the same inflorescence, and others are dioecious (each palm bears either male or female inflorescences). Some maintain male flowers for several days, and stagger their maturation; others mature all the male flowers on an inflorescence at once and drop them all within a day. *A priori*, the former are likely to be suitable for the development of insects, whereas the latter are not (Moore, 2001).

The caterpillars of Lepidoptera found in palm inflorescences are either herbivorous or detritivorous species. The plant feeding species range from those that feed purely on pollen in the male flowers, to those that feed on the structures of the male flowers, female flowers, developing nuts, and inflorescence branches. Obviously, these have different implications for the fecundity of the palms, and production of nuts where this is an economic consideration, e.g. coconuts. However, as yet very little is known about the ability of palms to compensate for insect damage to their inflorescences (Cock *et al.*, 1987; Waterhouse & Norris, 1987; Moore, 2001).

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The native palms of Trinidad and Tobago were treated by Comeau *et al.* (2003). There are 22 native species in 15 genera and they are an important feature of the country's landscape and biodiversity. Coconut is an introduced species in Trinidad of many years standing. It is found in cultivation throughout the island, usually near dwellings or former dwellings, but has not naturalised on any great scale.

This paper summarises published information on the Lepidoptera associated with the inflorescences of coconut and other palms in South America, and reports new observations from a preliminary survey of several indigenous and introduced palms in Trinidad, West Indies. The survey was focused on *Batrachedra nuciferae* Hodges (Lepidoptera: Batrachedridae), to establish its status and host range in Trinidad, to help assess the need and options for its management, as reported in Cock (2013). A second component of the survey was to collect information on what other species of small Lepidoptera feed on the same host palms as *B. nuciferae*, so that early stages and damage by *B. nuciferae* could be distinguished from those of other Lepidoptera. Here we present observations on the biology and host range of the Lepidoptera species associated with selected palms in Trinidad.

METHODS

A literature survey was made of the known palm-inflorescence feeding Lepidoptera in the Neotropical Region. This was based on key reference works (Lepesme, 1947; Howard *et al.*, 2001) and the references therein, and by searching CAB Abstracts to establish which species have been recorded from palm inflorescences in the area. Once the names of Lepidoptera species were found, further searches were made, including consulting the original descriptions and selected taxonomic and general works that might deal with these species, as well as internet searches, and relevant references compiled from these sources. The collection of the Natural History Museum, London (BMNH) was examined and biological and distribution data recorded for relevant species.

The field and laboratory methods and palms sampled are described in Cock (2013), and only outlined here. The fourteen species of palms that were sampled are presented in Table 1. Whole inflorescences and/or dropped male flowers were taken for each sample (Table 2). They were inspected visually in the laboratory, and caterpillars and cocoons on them were documented. The samples were then set up in emergence boxes for whole inflorescences or in plastic rearing containers for subsamples to rear out adult moths, which were recorded daily.

Because the field work was carried out during a short period in October 2011, it was not possible to sample all palm inflorescences at the same stage of development, and this will have affected the species and numbers of moths obtained. The condition of each sample is listed in Table 2 and notes on each sample are provided.

Samples of coconut flowers were obtained from five localities. Coconut is monoecious, and because it flowers continuously (Child, 1974), there was little difficulty taking samples with pollen-producing male flowers that were attracting insects.

The next seven species of palm are considered indigenous (Comeau *et al.*, 2003). Male and female flowers of *Attalea maripa* are born on separate inflorescences, but the floral biology and ecology of the genus is poorly understood and may vary with the age of the palm (Henderson *et al.*, 1995). The male flowers of *A. maripa* consist of little more than a bunch of pollen-bearing stamens, so they are very different in structure from all the other palms that we sampled. Although *A. maripa* was common at Bush Bush Island in Nariva Swamp, most palms were too tall to sample, and only an unopened spathe and an old dead male inflorescence from a shorter palm could be sampled. The unopened spathe was unblemished, with no signs of insect damage.

Bactris major is monoecious; the male flowers release pollen for about 24 hours and then are dropped immediately (Essig, 1971; Henderson, 1986). It seems likely that this short period of pollen-producing male flowers would make it very difficult for a pollen-feeding caterpillar to establish itself and survive. No trace of Lepidoptera feeding was found on the inflorescences sampled, and no moths were reared. Caterpillars, particularly of detritivorous species, theoretically could develop on the fallen flowers, but a 40ml sample of newly fallen flowers collected at the Botanic Gardens showed no signs of Lepidoptera feeding (visual inspection and dissection of ten flowers), and none were reared. *Bactris simplicifrons* has small inflorescences, each having only a few male and female flowers. We did not find any inflorescences with male flowers, but two inflorescences that had recently dropped their male flowers showed no trace of Lepidoptera or other insect damage.

All the male flowers had dropped, and only green developing nuts remained on the inflorescence sample of *Euterpe precatoria*. Examination of the branches from which the male flowers had dropped showed no signs of Lepidoptera damage, and specifically no sign of male flowers attached to the inflorescence by silk, or of cocoons. One of the hundreds of developing nuts was black rather than green and it contained

Table 1. The palms (Arecaceae) of which inflorescences were sampled, Trinidad, October 2011. Classification follows Dransfield *et al.* (2008) as presented by Trebrown Nurseries (2011); common names and their distributions are based on Comeau *et al.* (2003).

Subfamily, Tribe (subtribe)	Species	Common name in Trinidad	Distribution in Trinidad
Arecoideae, Areceae (Ptychospermatinae)	<i>Adonidia merrillii</i>	Manila palm	Introduced ornamental; widespread and common
Arecoideae, Areceae (Ptychospermatinae)	<i>Ptychosperma macarthurii</i>	Hurricane palm	Introduced ornamental; widespread and common
Arecoideae, Cocoseae (Attaleinae)	<i>Cocos nucifera</i>	Coconut	Introduced; cultivated in all except highest parts
Arecoideae, Cocoseae (Attaleinae)	<i>Attalea maripa</i>	Cocorite	Widespread except highest parts
Arecoideae, Cocoseae (Attaleinae)	<i>Syagrus romanzoffiana</i>	Queen palm	Introduced ornamental
Arecoideae, Cocoseae (Bactridinae)	<i>Bactris major</i>	Roseau, picmoc, black roseau	Widespread but absent from Northern Range and Long Stretch
Arecoideae, Cocoseae (Bactridinae)	<i>Bactris simplicifrons</i>	Yuyu	Local, scattered
Arecoideae, Cocoseae (Euterpeae)	<i>Euterpe oleracea</i>	Manac	Widespread at low elevations
Arecoideae, Roystoneae	<i>Roystonea oleracea</i>	Palmiste, royal palm, cabbage palm	Possibly introduced; S & E coasts, widespread as cultivated
Calamoideae Calameae (Calaminae)	<i>Calamus</i> sp.	Rattan palm	Introduced ornamental
Calamoideae, Lepidocaryae (Mauritiinae)	<i>Mauritia flexuosa</i>	Moriche	Local especially Nariva Swamp, Long Stretch
Coryphoideae, Sabaleae	<i>Sabal mauritiiformis</i>	Carat	South, widespread
Coryphoideae, Trachycarpeae (Livistoninae)	<i>Licuala spinosa</i>	Spiny licuala palm	Introduced ornamental
Coryphoideae, Trachycarpeae (unplaced)	<i>Pritchardia pacifica</i>	Fiji fan palm	Introduced ornamental

a small Lepidoptera caterpillar. It was not reared successfully and no moths were obtained from the emergence box.

Individual *Mauritia flexuosa* palms are dioecious; they bear inflorescences of either male or female flowers, not both (Ervig, 1993). We found one male palm at Aripo Savannah that was short enough to sample. It had several young, yellow-green inflorescences whose flowers had not yet opened, and several old dead, dark brown inflorescences; we collected one of each. The young inflorescence showed no sign of Lepidoptera damage when inspected, although moths were obtained by emergence box. Some feeding damage and very small caterpillars were found under the bracts of the old inflorescence, and adult moths were obtained by emergence box.

Roystonea oleracea is monoecious. An unusual feature of the genus is that from before the spathe

opens, it is packed with millions of very small, fluffy, branched hairs (Henderson *et al.*, 1995). We were able to sample one inflorescence from a relatively short palm at Kernahan. In this inflorescence, the male flowers had recently dropped and the female flowers were small. Many of the male flowers and the fluffy matrix were caught up in the inflorescence and the spathe, which remained in place below the inflorescence. More than 600 moths were reared from this one inflorescence. It seems likely that the fluffy matrix contained in inflorescences of *R. oleracea* provides a food source that can support many caterpillars of some of these moths, although we did not attempt to establish this.

Sabal mauritiiformis is unusual amongst the indigenous palms sampled in that the small flowers are bisexual (Henderson *et al.*, 1995), and hence they are not dropped once pollen production is complete. Two palms were examined at Kernahan; one had an

Table 2. Collections of palm inflorescences made in Trinidad, 8-18 October 2011. All sample sites were less than 50m asl.

Date	Palm species	Location	GPS	Details
8 Oct	<i>Adonidia merrillii</i> *	Curepe, CABI	N10°39.159 W61°24.065	1 inflorescence
12 Oct	<i>Attalea maripa</i>	Nariva Swamp, Bush Bush Is. (North)	N10°23.726 W61°02.381	1 unopened male inflorescence, 1 old male inflorescence
18 Oct	<i>Bactris major</i>	Botanic Gardens	N10 40°426 W61°30.913	Fallen male flowers
12 Oct	<i>Bactris major</i>	Nariva Swamp, Bush Bush Is. (North)	N10°23.730 W61°02.375	1 old inflorescence
14 Oct	<i>Bactris simplicifrons</i>	Nariva Swamp, Bush Bush Is. (South)	N10 23°390 W61°02.711	2 old inflorescence
18 Oct	<i>Calamus</i> sp.*	Botanic Gardens	N10 40°460 W61°30.888	2 old inflorescence
12 Oct	<i>Cocos nucifera</i>	Nariva Swamp, Bush Bush Is. (North)		1 inflorescence
10 Oct	<i>Cocos nucifera</i>	Centeno		Fallen male flowers
8 Oct	<i>Cocos nucifera</i>	Curepe, CABI (palm NL1)	N10°39.182 W61°24.069	1 inflorescence
8 Oct	<i>Cocos nucifera</i>	Curepe, CABI (palm TRT08)	N10°39.184 W61°24.074	1 inflorescence
8 Oct	<i>Cocos nucifera</i>	Curepe, CABI (palm TRT09)		1 inflorescence
12 Oct	<i>Cocos nucifera</i>	Nariva Swamp, Kernahan**	N10 21°490 W61°00.856	1 inflorescence
10 Oct	<i>Cocos nucifera</i>	Waller Field, Gafoor's Plantation	N10°39.177 W61°14.231	2 inflorescence
14 Oct	<i>Euterpe precatoria</i>	Aripo Savannah	N10 35°476 W61°11.338	1 old inflorescence
18 Oct	<i>Licuala spinosa</i> *	Botanic Gardens	N10 40°424 W61°30.913	1 old inflorescence
14 Oct	<i>Mauritia flexuosa</i>	Aripo Savannah, KP Quarry section	N10 36°352 W61°12.384	1 young inflorescence, 1 old inflorescence
18 Oct	<i>Pritchardia pacifica</i> *	Botanic Gardens	N10 40°427 W61°30.984	2 inflorescence (pooled)
18 Oct	<i>Ptychosperma macarthurii</i> *	Botanic Gardens	N10 40°423 W61°30.939	1 inflorescence
8 Oct	<i>Ptychosperma macarthurii</i> *	Curepe, CABI	N10°39.170 W61°24.086	several bits of inflorescence
18 Oct	<i>Roystonea oleracea</i>	Botanic Gardens	N10 40°428 W61°30.924	Fallen male flowers
12 Oct	<i>Roystonea oleracea</i>	Nariva Swamp, Kernahan**	N10 21°415 W61°00.869	1 inflorescence
12 Oct	<i>Sabal mauritiformis</i>	Nariva Swamp, Kernahan**	N10 22°207 W61°01.618	1 inflorescence
18 Oct	<i>Syagrus romanzoffiana</i> *	Botanic Gardens	N10 40°422 W61°30.933	1 inflorescence; fallen male flowers

*Introduced ornamental species.

**Also spelt Kernahan.

inflorescence that included open male flowers and this was sampled. Small caterpillars of a *Batrachedra* sp. were found.

The following six palms are introduced, ornamental species. *Adonidia merrillii* is monoecious, but the opening of the male flowers is staggered, so that only a few are open at a time. No sign of Lepidoptera feeding could be found in the inflorescence of the palms sampled, and none were obtained by emergence box.

Our sample of *Calamus* sp. in the Royal Botanic Gardens was two old, dry male inflorescences, comprising a densely packed mass of dry dead flowers. Examination showed some webbing and caterpillar frass in most parts of the inflorescence, and caterpillars with a dark head and dark purplish body were associated with this. Two cocoons were found but nothing emerged from these or in the emergence box, so we cannot confirm whether this species is a

suitable food plant for any of the Lepidoptera found in our survey, but certainly it is host to at least one species of Lepidoptera.

Licuala spinosa has bisexual flowers, and although each flower produces pollen only briefly, the inflorescence produces mature flowers over a period of about a month (Barfod *et al.*, 2003). We were able to obtain only an old inflorescence, from which most of the flowers were long gone, and on which some nuts were beginning to develop. The inflorescence showed no sign of Lepidoptera feeding, webbing or cocoons, but probably it was too old to expect to see this.

Pritchardia pacifica is monoecious. In addition to two inflorescences, we collected male flowers that had dropped and caught amongst the branches of an older inflorescence; there was light webbing and frass amongst these dropped male flowers and moths were obtained by emergence box.

Ptychosperma macarthurii is monoecious, and the male flowers are not synchronised. Thus we were able to find small numbers of scattered male flowers on the inflorescences that we sampled, and some flowers that dropped and got caught up between the inflorescence branches in one sample. There was no trace of webbing or frass on either the fresh or dropped male flowers, and no Lepidoptera were obtained by emergence box.

Syagrus romanzoffiana is monoecious but the one that we sampled had already dropped most of the male flowers. The inflorescence seemed completely healthy except that the ends of many apical secondary branches were trapped in the narrow apex of the spathe, together with many male flowers that had started to become mouldy. This situation seemed ideal for attack by Lepidoptera yet there was no trace of caterpillar damage. A small collection of dropped male flowers was also made from the base of the palm and set up separately. No Lepidoptera emerged from either sample.

Obtaining samples was a significant challenge, due to limited availability of flowers at the selected sites in the week of the survey, and those palms which were flowering were often too tall to sample safely. The samples obtained were not necessarily at the best stage to look for flower feeding caterpillars, especially those that feed on pollen, such as *Batrachedra* spp. Nevertheless, because Lepidoptera feeding leaves recognisable traces, such as webbing, frass and cocoons, old inflorescences where the dead male flowers were still present provided useful information.

Examination of inflorescences in the laboratory gave fairly reliable insight into the species present and their damage, but overlooked eggs or very young individuals, and risked overlooking very low density

populations. As a measure of population density, taking a sample at a single time point as we did, unavoidably makes no allowance for eggs that would have been laid in the inflorescence after collection, nor for moths that had already emerged before the sample was taken. By carefully examining the material before setting it up in the emergence box, we have a qualitative control for the latter aspect, but we could not control for the former.

Nevertheless, there was wide variation in the numbers of moths obtained from the emergence boxes, and large numbers of moths were obtained in several cases, so that this method does provide a time-efficient and cost-effective way to recognise the relative density of populations of Lepidoptera in the different inflorescences at the time of sampling. Any more rigorous approach would inevitably be much more expensive in time and money, so we believe this is a practical and appropriate approach.

RESULTS: LITERATURE SURVEY

Until recently, there has been little work on the Lepidoptera that breed in palm inflorescences in the Neotropical Region, and almost none of a general nature. Hence, the early work of Bondar (1940a, 1940b) in Bahia, Brazil, is still an important source of information on Lepidoptera that develop in the inflorescences of coconut (*Cocos nucifera*) and other palms. Bondar deals with *Batrachedra nuciferae* (as *B. perobtus* Meyrick, a misidentification), and two more damaging species: *Atheloca bondari* Heinrich (as *Hyalospila ptychis* Dyar, a misidentification or synonym, see below) and *Cadra cautella* (Walker) (as *Ephesia cautella*). In addition, there is limited information on a small number of other moths recorded from coconut, mostly noted by Lepesme (1947) in his standard reference *Les Insectes des Palmiers*. The summary by Moore (2001) in the recent equivalent title *Insects on Palms* (Howard *et al.*, 2001) adds very little for the Neotropical Region to what Bondar and Lepesme reported. Species not previously recorded from palm inflorescences were reared in this survey, and the available literature on these species is also summarised here. An overview of the literature survey is provided as Table 3.

Atheloca sp(p). (Pyralidae, Phycitinae)

Atheloca bondari was described by Heinrich (1956) in his revision of the American Phycitinae, based on Bondar's specimens in the United States National Museum. There is a very similar species, *A. subrufella* (Hulst) (= *Hyalospila ptychis*), found in Florida (USA),

Table 3. An overview of the Lepidoptera associated with palm inflorescences in the Neotropical Region, based on this literature review.

Species	Classification	Host plants	Feeding on	Distribution	Key references
<i>Anatrachyntis rileyi</i> (Walsingham)	Cosmopterigidae	Many plant hosts	Detritus	Old World origin, southern USA, Caribbean	Walsingham, 1882; Busck, 1917; Heinrich, 1921; Hodges, 1978; Zimmerman, 1978
<i>Atheloca bondari</i> (Heinrich)	Pyalidae, Phycitinae	<i>Cocos nucifera</i> , <i>Syagrus</i> spp., <i>Attalea</i> spp.	Male and female flowers	Brazil, Trinidad (this survey)	Bondar, 1940a, 1940b; Heinrich, 1956. As <i>A.</i> <i>subrufella</i> : Santana, 2008; Santana <i>et al.</i> , 2009, 2010, 2011
<i>Atheloca subrufella</i> (Hulst)	Pyalidae, Phycitinae	<i>Cocos nucifera</i> , <i>Sabal</i> <i>palmetto</i> , <i>Serenoa</i> <i>repens</i>	Male and female flowers	Florida, Caribbean (unconfirmed: French Guiana)	Heinrich, 1956; Kimball, 1965; Habeck & Nickersen, 1982; Schotman, 1989; Bento <i>et al.</i> , 2006
<i>Batrachedra nuciferae</i> Hodges	Batrachedridae	<i>Cocos nucifera</i> (unconfirmed: <i>Syagrus</i> spp., <i>Attalea</i> spp.)	Pollen of male flowers (unconfirmed: female flowers)	Brazil, Venezuela, Trinidad, probably widespread in South America	Bondar, 1940a, 1940b; Hodges, 1966; Arnal <i>et al.</i> , 1998; Sanchéz Soto, 2004; Sánchez-Soto & Nakano, 2002, 2004a, 2004b, 2008; Cock 2013
<i>Cadra cautella</i> (Walker)	Pyalidae, Phycitinae	Usually on stored products	Male and female flowers	Cosmopolitan	Bondar, 1940a, 1940b
<i>Erechthias minuscula</i> (Walsingham)	Tineidae, Erechthiinae	Many plant hosts	Detritus	Old World origin, southern USA, Caribbean	Walsingham, 1897; Swezey, 1909; Lepesme, 1947; Clarke, 1971; Zimmerman, 1978; Clarke, 1986
<i>Holcocera ochrobathra</i> (Meyrick)	Blastobasidae, Holcocerinae	<i>Cocos nucifera</i>	Detritus	Guyana, Florida	Meyrick 1921; Bodkin 1922; Adamski, 2002b; Heppner, 2003
<i>Phidotricha erigens</i> (Ragonot)	Pyalidae: Epipaschiinae	Polyphagous	Reproductive parts and leaves of diverse plants	Neotropical	Solis, 1993, 2011; Diniz & Morais, 2002
<i>Xystrologa nigrivitta</i> (Walsingham)	Tineidae, ?Meesiinae	Several plant hosts	Bracket fungus, <i>Roystonea oleracea</i> inflorescence (this survey); probably diverse materials	Caribbean	Davis <i>et al.</i> , 2012

Cuba and the Virgin Is., which differs primarily in the absence of 'a strong, dorsal, yellow hair tuft from the base of the male hind tibia' found only in *A. bondari* (Heinrich, 1956). Heinrich illustrates the male and female genitalia of *A. subrufella*, which show 'no essential differences' from those of *A. bondari*. Pictures of adult moths of *A. subrufella* can be seen at MPGNA (2012). Schotman (1989) reports *A. subrufella* from French Guiana and St. Lucia. Although the two species were considered distinct in Shaffer's (1995) treatment in the checklist of Neotropical Lepidoptera and though they do not seem to have been formally synonymised since (e.g. Beccaloni *et al.*, 2003), they are likely to be synonyms (M.A. Solis, pers. comm., 2012).

Nevertheless, we maintain both names here in line with formal taxonomy and pending a critical study of the question.

Bondar (1940a, 1940b) found that the caterpillars of *A. bondari* feed on both male and female flowers of coconut, as well as on the flowers of the native palms of the genera *Syagrus* (as *Cocos*) and *Attalea*. He illustrated the damage to male coconut flowers, which includes holes eaten through the sides of the male flowers; damage to the female flowers causes abortion or early nut fall.

Cabbage palm (*Sabal palmetto*) and saw palmetto (*Serenoa repens*) (Arecaceae) have been reported as food plants of *A. subrufella* in Florida (Kimball, 1965), and Habeck & Nickersen (1982) subsequently

described the biology on coconut thus: 'Larvae feed on newly emerged inflorescences and destroy flower buds and young developing coconuts. Coconuts up to 1.5 inches in diameter may be completely hollowed out. Larvae spin silk over the inflorescences ... and incorporate frass and plant material into the webs. Pupation occurs amid the plant material under the webbing.' Bento *et al.* (2006) describe the biology and mating behaviour in more detail. S.W.J. de Santana studied the life history and bioecology of *A. subrufella* in Pernambuco State, Brazil for her PhD thesis (Santana, 2008), and published accounts of the rearing method (Santana *et al.*, 2011), thermal biology (Santana *et al.*, 2010) and interaction with coconut mite, *Aceria guerreronis* Keifer (Santana *et al.*, 2009). Santana (2008) and Bento *et al.* (2006) both treat *Atheloca bondari* and the reports on its biology as though it is a synonym of *A. subrufella*.

***Cadra cautella* (Walker) (Pyralidae, Phycitinae)**

Cadra cautella is a well-known stored products pest found throughout tropical and temperate areas (Heinrich, 1956; Mound, 1989). Bondar (1940a, 1940b) reports that the caterpillars feed on male and female flowers of '*Cocos* spp.' (i.e. *C. nucifera* and *Syagrus* spp.) and *Attalea* spp. It should be noted that *Cadra* includes several similar species, with similar biology as stored product pests, and dissection of the genitalia is usually needed to confirm their identification (e.g. Goater, 1986; Mound, 1989); accordingly this identification needs species level confirmation. For the identification of the larvae, see Mound (1989) and Solis (2011).

***Phidotricha erigens* (Ragonot) (Pyralidae: Epipaschiinae)**

Phidotricha erigens, described from Puerto Rico (Ragonot, 1888), is found throughout the Caribbean and adjoining mainland, south to Brazil (Solis, 1993, 2011). In the past *P. erigens* has been treated as a synonym of *Pococera atramentalis* Lederer (1863). This would have been because *Phidotricha erigens* was identified as *Pococera atramentalis* in the collection of the Natural History Museum, London (BMNH). However, although the BMNH series of *Pococera atramentalis* are *Phidotricha erigens* (or were until curated), the holotype of *Pococera atramentalis* (also in the BMNH) is a different species (Solis, 1993).

Phidotricha erigens is known to be polyphagous on the leaves and reproductive parts of a wide variety of plants including Anacardiaceae, Calophyllaceae, Cucurbitaceae, Fabaceae, Oxalidaceae, Malvaceae,

Rutaceae, Passifloraceae, Phytolaccaceae, Poaceae, Rosaceae, Zingiberaceae (Solis, 1993, 2011), Burseraceae, Celastraceae, Erythroxylaceae, Fabaceae, Vochysiaceae (Diniz & Morais, 2002), Asparagaceae (Velázquez *et al.*, 2010), and Caryocaraceae (Carregaro, 2007), but not hitherto from Arecaceae. The possibility that these records represent several cryptic species with more specialised food plant preferences has not been investigated.

This species has previously been reported from Trinidad, based on specimens reared by F.W. Urich as *Pococera atramentalis* (Kaye & Lamont, 1927). Some of F.W. Urich's specimens are in the United States National Museum, Washington; they were reared in November 1922 from *Albizia saman* (Fabaceae). It also has been reared from flowers of *Tephrosia* sp. (Fabaceae), in October 1954 at St. Augustine, Trinidad, by F.D. Bennett (specimen in University of the West Indies Zoology Museum). The species occurs also in Tobago (M.J.W. Cock unpublished).

***Batrachedra* spp. (Batrachedridae)**

The genus *Batrachedra* is usually placed in the family Batrachedridae of the Gelechioidea (Hodges, 1999; Brown *et al.*, 2004; Kaila *et al.*, 2011; van Nieukerken *et al.*, 2011), but has also been placed in the subfamily Batrachedrinae of the Coleophoridae (Becker, 1984; Kaila, 2004). The family Batrachedridae is considered paraphyletic (Kaila, 2004; Kaila *et al.*, 2011), so further changes may follow.

Hodges (1966) revised the American *Batrachedra* spp. and recognised three groups of species within the genus. One of these groups includes three species feeding on palm inflorescences, one feeding on the base of the pineapple fruiting body, and six of unknown biology. Positive identification of these species is only possible based on dissection and examination of the genitalia, those of the female being more diagnostic than those of the male. *Batrachedra nuciferae* is discussed below; *B. mathesoni* Busck occurs in Florida and the caterpillars feed on coconut flowers; and *B. decoctor* Hodges also occurs in Florida where the palm *Serenoa repens* is a food plant. Other *Batrachedra* spp. of this group have been described from Puerto Rico, Jamaica, St Lucia and Central America, etc. *Batrachedra arenosella* (Walker) is the name applied to a *Batrachedra* species in South-East Asia and Australasia which also has been reported to feed on coconut inflorescence, causing insignificant damage (Corbett & Gater, 1924; Kalshoven & van den Laan, 1981). However, most probably this name is incorrectly applied, as *B. arenosella* was described from New Zealand, where it is known as a scale predator (Moore, 2001).

At least two species of *Batrachedra* feed as caterpillars in the inflorescences of palms in Trinidad (Cock, 2013), *B. nuciferae* on coconut and *Roystonea oleracea*, and an unidentified species on *Sabal mauritiformis*. It seems likely that other species of this group of American *Batrachedra* spp. will be found to feed on palms, probably showing some specialisation as to species or genera that are acceptable as food plants.

***Batrachedra nuciferae* Hodges (Batrachedridae)**

Batrachedra nuciferae was first recognised by Bondar (1940a, 1940b) who described its biology in Bahia State, Brazil (as *B. perobtusa*). It was subsequently described as a new taxon, based on Bondar's material reared from male coconut flowers, in Hodges' (1966) revision of the American *Batrachedra*. The species description was based only on material reared from coconut and Hodges did not refer to material from the other palms which Bondar (1940a, 1940b) records as food plants. Moore (2001) summarises Bondar's observations under the name *Ifeda perobtusa*, overlooking the name change in Hodges' (1966) revision. In 1998, *B. nuciferae* was recorded from Venezuela as a new pest of coconut (Arnal *et al.*, 1998). In 2006, *B. nuciferae* was correctly reported from Trinidad as a new pest of coconut (MALMR, 2006, 2008), although the adult moth shown in MALMR (2008) is *Anatrachyntis rileyi* (Walsingham) (reported below as reared from palm inflorescences).

Bondar (1940a, 1940b) reported that the caterpillars of *B. nuciferae* rest in the male flowers of coconut where they feed on pollen, and they are also common in the flowers of several other palms: *Syagrus coronata* (= *Cocos coronata*), *S. vagans* (= *C. vagans*), *S. schizophylla* (= *C. schizophylla*), *Attalea funifera* and *A. piassabossu*. He considered that the damage to male flowers reduced the probability of fertilization of female flowers and hence could adversely affect nut production, but presented no evidence for this conclusion. He gives brief descriptions of the caterpillar and pupa, states that the cocoon is formed on a solid substrate or amongst the fallen male flowers in the leaf axil below, and that the life cycle takes 15-18 days.

Since 1940, there was almost no published work on the coconut moth, until the work of S. Sánchez-Soto in São Paulo State, Brazil, this century. The moth was the subject of his research thesis (Sánchez Soto, 2004) and publications on the distribution (Sánchez-Soto & Nakano, 2002, 2004a), morphology (Sánchez-Soto & Nakano, 2004b), and biology (Sánchez-Soto & Nakano, 2008). The egg, caterpillar (including chaetotaxy), pupa and adult are illustrated in both Sánchez Soto (2004) and Sánchez-Soto & Nakano (2004b).

Arnal *et al.* (1998) reported the presence of the moth in several parts of Venezuela. Carneiro *et al.* (2004) stated that in the Município de Parnaíba, Piauí, north-east Brazil, the caterpillars eat both male and female flowers. Observations from Trinidad were reported by Cock (2013), who found no evidence that female flowers were damaged. His observations showed that the inflorescence of *Roystonea oleracea* is also used as a food source, but that no *B. nuciferae* were obtained from inflorescences sampled from 12 other indigenous and introduced palms, including *Attalea maripa*.

***Holcocera ochrobathra* (Meyrick) (Blastobasidae, Holcocerinae)**

Although some recent works treat Blastobasidae as a subfamily of Coleophoridae (Hodges, 1999), it is retained as a family here in line with van Nieukerken *et al.* (2011). Species of Blastobasidae are usually considered to be scavengers or detritivores on a variety of substrates, but some are herbivorous (Adamski & Brown, 1989). The North American species have been revised and arranged in two subfamilies and several genera (Adamski & Brown, 1989), but the South American species are still poorly known (Adamski, 2002b), apart from those of Costa Rica (Adamski, 2002a, 2013). There are many undescribed species (Adamski & Brown, 1989; Adamski, 2002b).

Meyrick (1921) described *H. ochrobathra* from Guyana, in the genus *Blastobasis*, based on specimens reared from coconut flowers by L.D. Cleare Jr. in 1920, and stated that the type was in the 'Brit. Mus.' (BMNH). There are four such specimens in the BMNH, of which a male is designated lectotype and has been dissected and illustrated by Clarke (1963), and a female has been designated paralectotype. Adamski (2002b) reported four further paratypes in the US National Museum. In the British Guiana Department of Science and Agriculture Annual Report for 1920, Bodkin (1922, as abstracted in *Review of Applied Entomology*) reported "In one district the blossoms of the palms were found to be infested by the larvae of a small moth, *Blastobasis ochrobathra*, Meyr." Although this species did not appear in the Lepidoptera of North America checklist (Hodges *et al.*, 1983), it is recorded from Florida (Heppner, 2003). In his synopsis of the Neotropical Blastobasidae, Adamski (2002b) transferred *ochrobathra* to *Holcocera*, but noted that it is known only from the type locality. Heppner (2003) placed this species in *Blastobasis* rather than *Holcocera*, but we follow Adamski (2002b) here. We note that there is a Barbados specimen in the BMNH reared

from castor oil seeds by R.W.E. Tucker, December 1937, although its identity has not been confirmed by dissection.

There is a similar species, *H. grenadensis* (Walsingham, 1891), described from Grenada. The female lectotype and four paralectotypes from Grenada and Dominica are in the BMNH (Adamski, 2002b), together with specimens from Barbados and the Bahamas, which have not been dissected to confirm their identity. Adamski (1998) treated this species and transferred it to the genus *Holcocera*. Some authorities still (or again) place it in *Blastobasis* (e.g. Lee & Brown, 2009a), but we follow Adamski's (2002b) treatment here. On external appearance, *H. grenadensis* differs from *H. ochrobathra* primarily in that the forewings are irregularly streaked with pale brown scales (Adamski, 2002b), but both species are variable. The two species can also be differentiated by characters of the genitalia (Adamski, 2002b). The male and female genitalia have been figured (Clarke, 1963; Adamski, 1998, 2002b). Given the general similarities of species in this subfamily, even between genera, support from DNA barcoding (Hajibabaei, *et al.*, 2007; Janzen *et al.*, 2009; Adamski *et al.*, 2010) might simplify identifications in future.

Anatrachyntis rileyi (Walsingham) (Cosmopterigidae)

Anatrachyntis (Meyrick, 1915a) is a genus of more than 50 species of small moths, almost exclusively from the Old World. The species of known biology seem to be scavengers and several have been associated with palm inflorescences. *Anatrachyntis simplex* (Walsingham) was described from Africa, but is now found in many parts of the tropics, and recognised as a polyphagous scavenger on various crops including cotton and coconut (Lepesme, 1947). Other species of this genus have been recognised as feeding on coconut flowers in the Old World, including, *A. paroditis* (Meyrick) in South-east Asia (Corbett, 1922), the Pacific (Lever, 1938), and the Seychelles (Vesey-Fitzgerald, 1941) etc., and *A. dactyliota* (Meyrick) is recorded in Malaysia (Meyrick, 1931).

Although *A. rileyi* was described from Georgia, USA (Walsingham, 1882), and is known from the USA and several Caribbean Islands, it is likely to be of Old World origin, perhaps from Africa (Meyrick, 1915a, p. 326; Zimmerman, 1978) and is widespread from southern Asia through the Pacific. At different times it has been placed in the genera: *Batrachedra* (Walsingham, 1882), *Sathrobrotia* (Hodges, 1962), and *Pyroderces* (Hodges, 1978). At about the same time that Hodges (1978) placed *rileyi* in *Pyroderces* in his treatment of the family in the standard reference *The*

Moths of America North of Mexico, Zimmerman (1978) transferred *rileyi* to *Anatrachyntis*. The latter has become accepted by European authors (e.g. Koster & Sinev, 2003; Heckford & Sterling, 2004), while *Pyroderces* is still commonly used in North America (e.g. Lee & Brown, 2009b).

There is a similar species, *A. badia* (Hodges) in the USA, which was described in 1962 and has a similar range of food materials but with little documented overlap of actual food plant species (Hodges, 1962); the two are separated by markings on the hind leg tibia (Hodges, 1978). Where the two species occur together they could easily be confused, and this would have been the case with publications from the first half of the 20th century (Zimmerman, 1978). The caterpillars of *P. rileyi* have been described by Busck (1917) and Heinrich (1921) and those of *P. badia* by Adamski *et al.* (2006), who could find no diagnostic characters to separate caterpillars of the two species.

The caterpillars are detritivores reared from a wide variety of plant materials including cotton bolls (Walsingham, 1882; Busck, 1917; Heinrich, 1921), as well as flowers, beans and pods of *Ricinus* (castor oil; Euphorbiaceae), flowers of *Hyptis* sp. (Lamiaceae), *Colocasia esculenta* (dasheen; Araceae), maize (corn husks and tassels, stored corn), many kinds of old leguminous pods, aloe, coffee beans, coffee cherries, eggplant, banana, dead *Panicum torridum*, pineapple (dried parts, fruits, stored seeds), *Rochea* (Crassulaceae), *Samanea saman* (Fabaceae-Mimosoideae), *Sapindus oahuensis* (Sapindaceae), and tamarind (Hodges, 1962, 1978; Zimmerman, 1978; Garraway *et al.*, 2007). Although *A. badia* has been reported from 'blossoms of coconut' in Florida (Hodges, 1962), here *A. rileyi* is reported from coconut inflorescence for the first time.

Erechthias minuscula (Walsingham) (Tineidae, Erechthiinae)

Erechthias minuscula was described from Jamaica, the Virgin Islands and Grenada (Walsingham, 1897), and it is known from various Caribbean Islands (Clarke, 1971, 1986; specimens in the BMNH), North America (MPGNA, 2012), Africa, southern Asia and the Pacific (Lepesme, 1947; Clarke, 1971; Zimmerman, 1978; Clarke, 1986). Meyrick (1915b, p. 367) considered that it is probably Oriental in origin, and therefore introduced in Africa, the Americas and Pacific. It is predominantly a detritus feeder found associated with dead or decaying tissue of a wide range of plants from many families (Swezey, 1909, 1910; Lepesme, 1947; Clarke, 1971; Zimmerman, 1978; Plumbley & Rees, 1983; Clarke, 1986; material in

BMNH), including coconut (Lepesme, 1947; material in BMNH from Fiji and the Solomon Islands). It is also recorded as a predator or scavenger of scale insects, especially *Pseudaulacaspis pentagona* (Targioni-Tozzetti), *Lepidosaphes pinnaeformis* (Bouché), *Icerya purchasi* Maskell, *Aspidoproctus bouvieri* Vayssière, and *Orthezia insignis* Browne (Swezey, 1909; Lepesme, 1947). In contrast to all other reports, Harris (1935) stated that 'there is no doubt as to its ability to feed on living coconut tissues' in Tanzania, but this has not been confirmed.

A related species, *E. flavistriata* (Walsingham) found from South-East Asia and the Pacific, has been recorded from coconut flowers (Meyrick, 1928), but is primarily associated with leaf sheaths, dead leaves and fibrous parts from a variety of plants, but in particular sugar cane (Zimmermann, 1978).

***Xystrologa nigrivitta* (Walsingham) (Tineidae, ?Meesiinae)**

The following is based on a recent paper on the West Indian species of *Xystrologa* by Davis *et al.* (2012). This Neotropical genus comprises six described and several undescribed species. Two species occur in the West Indies: *X. grenadella* (Walsingham) and *X. nigrivitta*. The former has been reared from branches of *Sabal causiarum* (Arecaceae) in Bermuda, from bark mulch used as a potting media and roots of orchids in nurseries in Florida, from damaged areas on the trunks of bonsai *Ficus* trees in Florida, on the roots of pineapple in Puerto Rico, and pupae have been found under bark of an unidentified tree in Dominica. As an introduced species in Germany, it was recently reared from caterpillars 'found in dead wet wood of *Robinia*, on which are arranged *Tillandsia* and other Bromeliaceae, and on palm (*Washingtonia* sp.)' in a large greenhouse.

Xystrologa nigrivitta has been reared from an unidentified bracket fungus in Dominica, but has not previously been associated with a palm inflorescence. Thus, the available records point to members of this genus being opportunistic detritivores. *Xystrologa nigrivitta* is known from several West Indian Islands, including Trinidad, and it probably occurs throughout the West Indies. It was reared from the inflorescence of *Roystonea oleracea* in the survey reported below.

Other species

Lepesme (1947) includes a record of *Tirathaba complexa* (Butler) (= *Harpagoneura complexa*) (Pyralidae, Galleriinae) from Brazil. This is one of several species names included under the common name coconut

spike moth, but it is unclear whether this includes several similar species or one variable species under the general name *T. rufivena* (Walker) (Waterhouse & Norris, 1987). This species or group of species from South-East Asia and the Pacific is considered a pest of coconut inflorescence, although the impact on yield is questionable (Corbett, 1931; Taylor, 1930; Cock *et al.*, 1987; Waterhouse & Norris, 1987). However, the record from Brazil is likely to be an error or misidentification, as there have been no subsequent observations of this relatively conspicuous inflorescence feeder from South America.

Additional species recorded below, for which there is no published information include a species of Gelechiidae reared from *Attalea maripa* and two species of Cosmopterigidae reared from *A. maripa* and *Mauritia flexuosa*.

RESULTS: FIELD SURVEY AND LAB WORK IN TRINIDAD

More than one thousand moths of 12 species were reared from six of the 14 palm species (Table 4). Moths emerged from the samples for up to two months after collection of the inflorescence sample (Fig. 1).

***Atheloca bondari* Heinrich (Pyralidae, Phycitinae) (Fig. 2a)**

Adults of *A. bondari* were identified as an *Atheloca* sp. from the photographs on MPGNA (2012), and to species from Heinrich (1956). The Trinidad specimens have the strong hair tuft at the base of the hind leg tibia, which is the distinguishing character for *A. bondari*, and absent in *A. subrufella* (Heinrich, 1956). Accordingly, this species is treated as *A. bondari*, although it is recognised that this may prove to be a synonym of *A. subrufella* (see literature review).

This species was reared from *Roystonea oleracea* at Kernahan, Nariva Swamp. The caterpillars were characterised as having a dark brown head and pronotum, purple-brown body with paler dorsal and lateral lines (Fig. 4), but these preliminary observations need confirmation based on systematic rearing of documented individual caterpillars. Caterpillars were observed to make webbing amongst flowers, tie together dead flowers, and feed amongst the fluffy padding of *R. oleracea* inflorescences and on male flowers. Caterpillars are larger than those of *Batrachedra nuciferae* and produce correspondingly larger frass.

Similar caterpillars were found on coconut at Curepe, but none were individually reared successfully

Table 4. Summary of moths reared from palm inflorescences. No moths were reared from *Adonidia merrillii* (Curepe, CABI), *Bactris major* (Bush Bush Island, Botanic Gardens), *Bactris simplicifrons* (Bush Bush Island), *Calamus* sp. (Botanic Gardens), *Euterpe precatoria* (Aripo Savannah), *Licuala spinosa* (Botanic Gardens), *Ptychosperma macarthurii* (Curepe, CABI; Botanic Gardens), or *Syagrus romanzoffiana* (Botanic Gardens). In addition, a single specimen of *Phidotriza erigens* was reared from the young male inflorescence of *Mauritia flexuosa*.

Palm species	Location	<i>Atheloca bondari</i>	<i>Neodavisia</i> sp.	<i>Batrachedra nuciferae</i>	<i>Batrachedra</i> sp.	<i>Holcocera</i> sp.(p).	<i>Anatrachyntis rileyi</i>	<i>Erechthias minuscula</i>	<i>Xystrologa nigrovittata</i>	Unidentified Gelechiidae	Unidentified Cosmopterigidae 1	Unidentified Cosmopterigidae 2	Total
<i>Attalea maripa</i> (old male)	Bush Bush Is. (North)		26							11	21		58
<i>Cocos nucifera</i> (combined)	Curepe, CABI			40		10	15	1					66
<i>Cocos nucifera</i>	Centeno			20			1	1					22
<i>Cocos nucifera</i> (combined)	Waller Field			121			116	7					244
<i>Cocos nucifera</i>	Bush Bush Is. (North)			1									1
<i>Cocos nucifera</i>	Kernahan	1		26									27
<i>Mauritia flexuosa</i> (old male)	Aripo Savannah											52	52
<i>Mauritia flexuosa</i> (young male)	Aripo Savannah					8	1						9
<i>Pritchardia pacifica</i> *	Botanic Gardens						16	3					19
<i>Roystonea oleracea</i>	Kernahan	10		57		16	41	339	135				598
<i>Roystonea oleracea</i>	Botanic Gardens						2	2					4
<i>Sabal mauritiformis</i>	Kernahan				12								12
TOTAL		11	26	265	12	34	192	353	135	11	21	52	1,112

* Introduced ornamental species.

to confirm the identification. One adult was reared from a caterpillar isolated from coconut at Kernahan; amongst the terminal male flowers of one secondary inflorescence branch, it had tied three dead male flowers to the branch with silk. Since *A. bondari* is reported to attack coconut inflorescences (Bondar, 1940a, 1940b; Heinrich, 1956) it seems safe to anticipate that this species does attack coconut more widely in Trinidad, although not as frequently as some of the other species considered here, such as *B. nuciferae*. Furthermore, as noted by Bondar (1940a, 1940b), the caterpillar is more damaging than that of *B. nuciferae*, causing direct damage to male and female flowers.

Cocoons are formed completely enclosed in loose debris, but were not distinguished from those of *Anatrachyntis rileyi*. The adult moths are typical

phycitine moths (Fig. 2a), and no other members of this subfamily were obtained in our survey.

Phidotriza erigens (Ragonot) (Pyralidae, Epipaschiinae) (Fig. 2b)

This species (Fig. 2b) was reared just once from old, dead male inflorescence of *Mauritia flexuosa*. Given the range of alternative hosts reported, it is probably an occasional facultative herbivore or detritivore in palm inflorescences.

Neodavisia sp. (Pyralidae, Pyralinae) (Fig. 2c)

This appears to be an undescribed species, probably in the genus *Neodavisia* (Fig. 2c); it will be

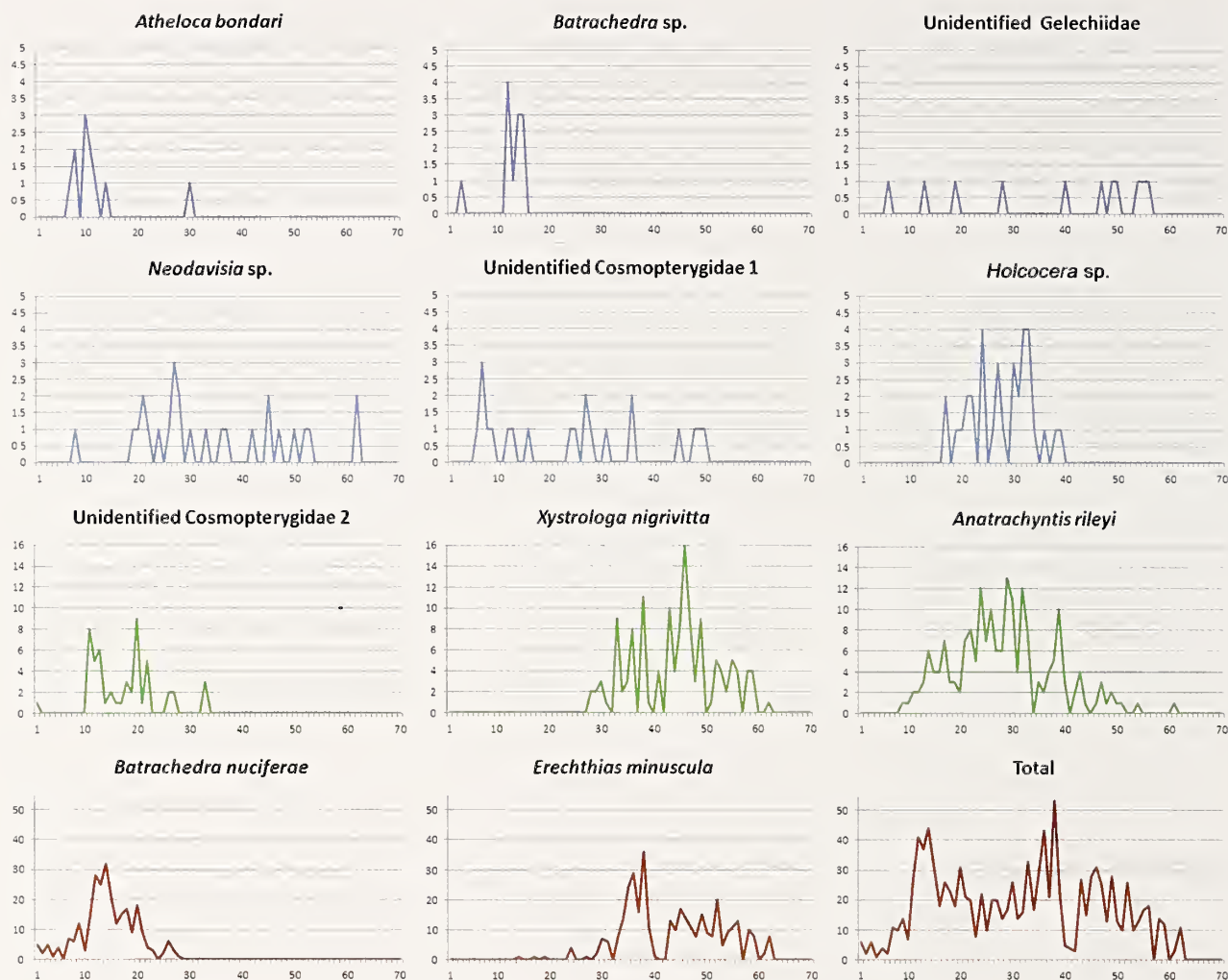


Figure 1. Number of moths emerging daily, counting from the day of sample collection. Results are pooled for all collections. Each colour line is related to a different axis scale. The single specimen of *Phidotriza erigens* is not shown; it emerged 27 days after the inflorescence was collected.

described in a forthcoming paper dealing with this and two similar, perhaps synonymous, genera from the Americas (M.A. Solis, pers. comm., 2012). It was reared from the dead male inflorescence of *Attalea maripa* and associated with dark caterpillars similar to those of *Atheloca bondari* and *Xystrologa nigrivitta* feeding amongst the stamens, and cocoons spun up amongst and completely covered by the stamens. Because the inflorescence was old and dead, most likely the caterpillars feed on dead plant material.

***Batrachedra nuciferae* Hodges (Batrachedridae) (Figs. 2d, 3b)**

Cock (2013) reports observations on *B. nuciferae* from this survey, and illustrates the early stages.

Caterpillars were found on coconut and *Roystonea oleracea*, but not on other palms; they were considered to be primarily restricted to the male flowers in which they are pollen feeders.

***Batrachedra* sp. unidentified (Batrachedridae) (Fig. 2e)**

This species was reared from carat palm, *Sabal mauritiiformis*, at Kernahan, Nariva Swamp. It resembles *B. nuciferae*, but is significantly smaller (Fig. 2d). Examination of parts of the inflorescence that included open flowers revealed webbing and frass, forming a protective tunnel or tube on the stem (Fig. 5). At one end this tunnel covered a shallow groove in the inflorescence branch, and the webbing here incorporated yellow debris from the branch in a more

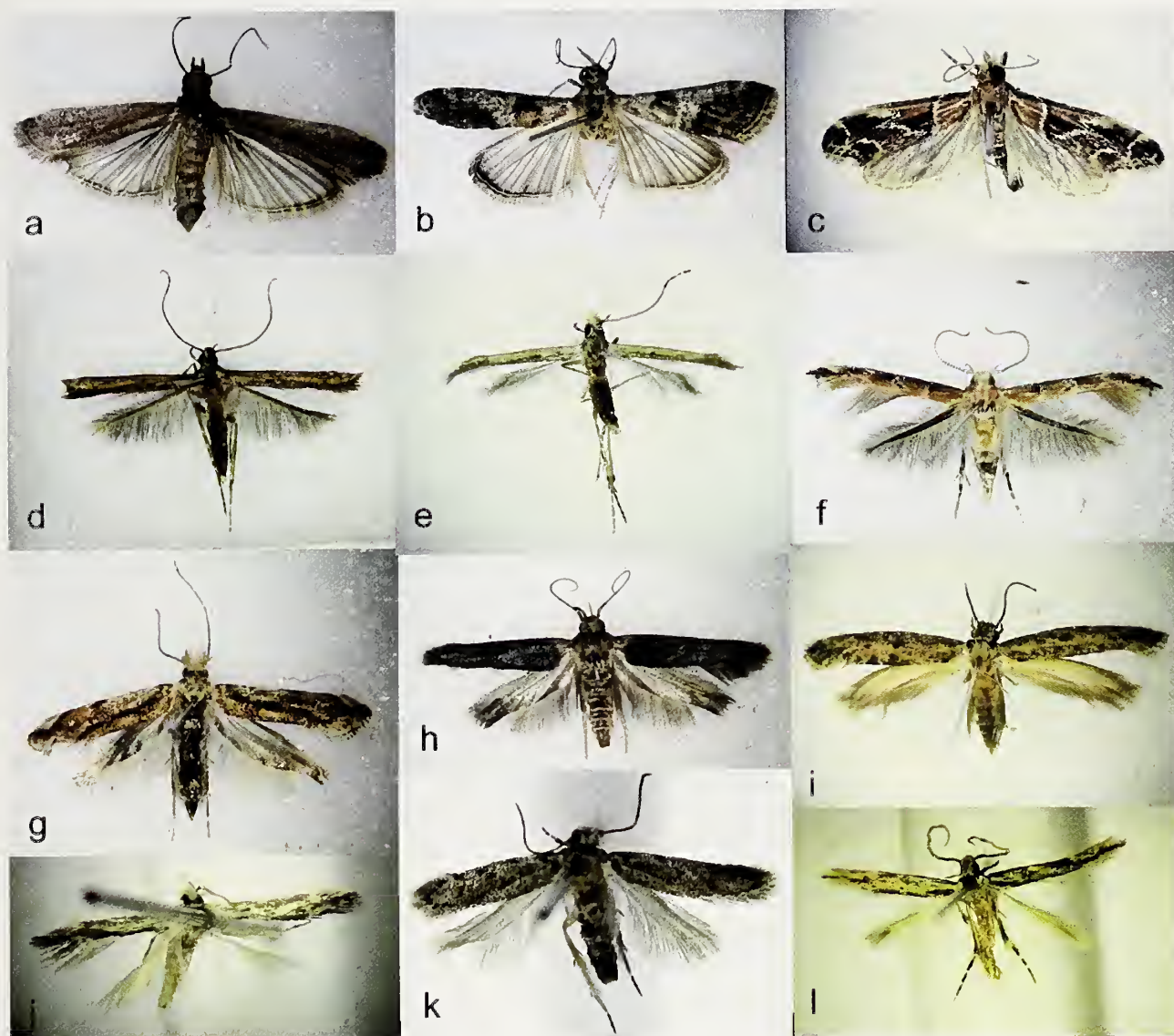


Figure 2. Pinned moths reared from palm inflorescences, Trinidad, Oct 2011; not to scale, the wingspan for each is given; **a**, *Atheloca bondari*, male, 16.6mm; **b**, *Phidotricha erigens*, 9.7mm; **c**, *Neodavisia* sp., 10.5mm; **d**, *Batrachedra nuciferae*, 10mm; **e**, *Batrachedra* sp. indet. reared from *Sabal mauritiformis*, 7mm; **f**, *Anatrachyntis rileyi*, 9mm; **g**, *Erechthias minuscula* female, 9.7mm; **h**, *Holcocera* sp., 13.7mm; **i**, *Xystrologa nigrivitta* female, 8.0mm; **j**, unidentified Cosmopterigidae sp. 2 (from *Mauritia flexuosa*), 5.2mm.; **k**, unidentified Gelechiidae (from *Attalea maripa*), 8.9mm; **l**, unidentified Cosmopterigidae sp. 1 (from *Attalea maripa*), 5.5mm

or less continuous cover or shelter. The remainder of the tunnel was more transparent, with scattered frass incorporated. Each tunnel sheltered a small pale caterpillar, resembling those of *B. nuciferae*, but smaller and with the head and pronotum pale brown. These caterpillars bore into the base of individual flowers and move from flower to flower, mostly in their tunnels. In due course some of these caterpillars made cocoons in the style of *B. nuciferae*, but smaller. The adult is similar to that of *B. nuciferae*

(fig. 2d) but smaller. Three adults were reared from these caterpillars and a further nine by emergence box over two weeks.

***Holcocera* sp. (Meyrick) (Blastobasidae, Holcocerinae) (Fig. 2h)**

A *Holcocera* sp. was reared in this survey from inflorescences of three palm species: coconut, *Roystonea oleracea* and dead male inflorescence of

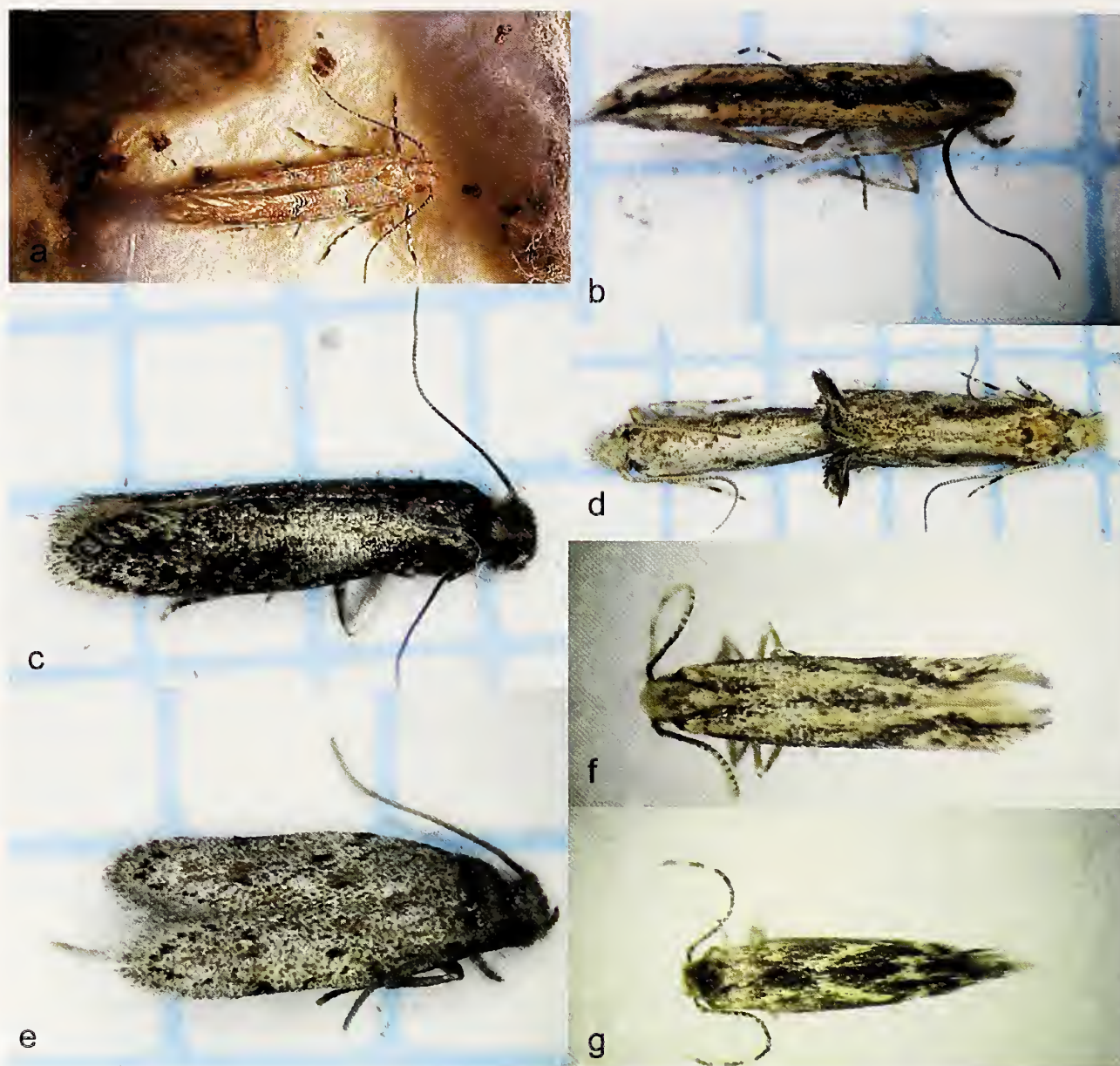


Figure 3. Dead moths (except for photo a, which was alive) in more or less normal resting positions, reared from palm inflorescences, Trinidad, Oct 2011; not to scale, see legend to Figure 2 for wingspans; scale squares = 2mm. a, living *Anatrachyntis rileyi*; b, *Batrachedra nuciferae*; c, *Xystrologa nigrivitta*; d, *Erechthias minuscula* mating pair; e, unidentified Gelechiidae (from *Attalea maripa*); f, unidentified Cosmopterigidae sp. 1 (from *Attalea maripa*); g, unidentified Cosmopterigidae sp. 2 (from *Mauritia flexuosa*). Figure a (from MALMR 2008), photo by Research Division Central Experimental Station, Centeno, Trinidad and Tobago.

Mauritia flexuosa. Specimens were identified as an unknown *Holcocera* sp. by D. Adamski, United States Department of Agriculture. The first author examined the male genitalia of a specimen from each palm and considered them to represent just one species, closely related to, but apparently distinct from, *H. ocreobathra*, the species described from coconut flowers in Guyana,

and *H. grenadensis*, described from Grenada and Dominica (see literature review).

Caterpillars of this species were found on and reared from amongst the fluffy matrix and dead male flowers of *R. oleracea* at Kernahan, but we did not establish which part of this served as their food source. They were characterised as similar to those

of *Atheloca bondari* (Fig. 4) but darker. *Holcocera* spp. generally feed on detritus and dead plant material, and this is probably the role of this species in palm inflorescences. The cocoons were not distinguished from those of *A. bondari*. The adults (Fig. 2h) are easily distinguished from the other species obtained in this survey by their wing shape and colour.

***Anatrachyntis rileyi* (Walsingham) (Cosmopterigidae) (Figs. 2f, 3a)**

This species was initially identified by comparison with the type and the BMNH series. All specimens were checked against the diagnostic features in Hodges (1978, p. 47), to ensure that no *A. badia* were present. A subsample of pinned moths was examined by D.R. Davis, Smithsonian Institution, who confirmed their identity. The adult of this moth (Fig. 3a) was illustrated incorrectly as *Batrachedra nuciferae* in MALMR (2008). It is attractively coloured and marked in tones of orange and brown (Figs. 2f, 3a) and easily distinguished amongst the moths reared from the survey.

In this survey, *A. rileyi* was reared from the inflorescences of five palm species (Table 4). The caterpillar was characterised as having the head chestnut brown, pronotum and anal plate brown, body pink-brown (Fig. 6), but these preliminary observations need confirmation based on systematic rearing of documented individual caterpillars, an exercise beyond our resources on this occasion. The cocoon was similar to that of *Atheloca bondari*, but smaller. The exact food and feeding style was not established, but the record from dead male inflorescence of *M. flexuosa*, and the fact that adults emerged later from the emergence boxes than did those of the pollen-feeding *B. nuciferae*, supports the expectation that it feeds on dead plant material, as has been previously documented.

***Erechthias minuscula* (Walsingham) (Tineidae, Erechthiinae) (Figs. 2g, 3d)**

This species was initially identified by comparison with the BMNH series. A subsample was examined by D.R. Davis, Smithsonian Institute, who confirmed this identification. It was obtained from Kernahan by emergence box from *Roystonea oleracea* in large numbers and once from coconut (Table 4). Amongst the material reared, it was distinctive due to the reflexed wing tips (Fig. 3d).

Early stages have not been unequivocally associated, but caterpillars found on coconut at Kernahan (Fig. 7) are likely to be this species. This caterpillar webbed



Figure 4. Caterpillar of *Atheloca bondari* amongst dropped male flowers and fluffy matrix of inflorescence of palmiste, *Roystonea oleracea*, Kernahan.



Figure 5. Caterpillars and signs of *Batrachedra* sp. indet. on carat palm, *Sabal mauritiformis*, Kernahan. Note the webbing and frass to the right.



Figure 6. Caterpillar of *Anatrachyntis rileyi* amongst silk webbing on dropped male flowers of palmiste, *Roystonea oleracea*, Kernahan.



Figure 7. Provisionally associated early stages of *Erechthias minuscula* on coconut, Kernahan. **a**, dead male flowers attached to inflorescence with silk webbing; **b**, caterpillar, dorsolateral view.

together dead male flowers attaching them to the inflorescence branch, sometimes in a pendulous chain (Fig. 7a). One had attached a dead male flower to the base of a female flower, and although the female flower was marked, it did not appear to have been significantly damaged on this occasion. These caterpillars were characterised as having a chestnut brown head, dark brown pronotum with a narrow pale dorsal line, body dull pale brown with darker dorsal, dorsolateral and lateral longitudinal lines; body with erect setae with the base dark.

Xystrologa nigrivitta (Walsingham) (Tineidae, ?Meesiinae) (Figs. 2i, 3c)

This species was reared commonly from the inflorescence of *Roystonea oleracea* from Kernahan (Table 4). Emergence did not start until a month after the inflorescence was collected (Fig. 1). No observations were made on the early stages, but given the known biology of the genus (Davis *et al.*, 2012) they are likely to be detritivores in inflorescences of *R. oleracea*.

Unidentified Cosmopterigidae sp. 1 and Gelechiidae sp. from *Attalea maripa* (Figs. 2k, 2l, 3e, 3f)

Two more species were reared from the old dead male inflorescence of *Attalea maripa*, where they were probably feeding on dead plant material. The old male inflorescence, in which the flower parts, including the long pollen-bearing stamens, were completely dead and dry, showing a great deal of old feeding damage by Lepidoptera, based on the amount of frass and webbing that was observed (Fig. 8). The flower remains contained many small 3mm long, plain white Lepidoptera cocoons, which were associated with an unidentified Cosmopterigidae species (sp. 1, Figs. 2l, 3f) obtained by emergence box. An unidentified species of Gelechiidae (Figs. 2k, 3e) was obtained by emergence box only. The relative contribution of the different species reared to the damage observed is not clear. Although no other distinctive remains in terms of cocoons were found when examining the inflorescence, it is possible that additional species may have completed development and emerged and dispersed before our sample was taken.

In addition to these small species, a long, tough silk-lined gallery or tunnel was found running through the dry mass of stamens, more than 30cm long and in places 1cm in diameter (Fig. 9). A cast head capsule, 2.4mm wide x 2.7mm high, was found in this gallery. No other sign of the caterpillar or its pupa were found, but we assume it was the maker of this tunnel. The purpose of the tunnel and life style of the

caterpillar that made it is open to speculation. The tunnel would probably provide protection from small vertebrate predators that are likely to be attracted to the large number of caterpillars in the inflorescence. It would enable the inhabitant to move around safely over long distances within the inflorescence; could the builder be a predator itself?

Unidentified Cosmopterigidae sp. 2 from *Mauritia flexuosa* (Figs. 2j, 3g)

Some feeding damage and very small caterpillars were found under the bracts of the old male inflorescence of *Mauritia flexuosa*. More than 50 moths of a very small unidentified Cosmopterigidae species (sp. 2, Figs. 2j, 3g) were subsequently reared by emergence box from the old male inflorescence, but not from the young inflorescence sampled from the same palm. We suppose that caterpillars of this species feed as detritivores on dead plant tissue in the old inflorescence.

DISCUSSION AND CONCLUSIONS

In total, more than one thousand moths of 12 species were reared from six of the 14 palm species sampled (Table 4). All the previously reported genera of palm-feeding Lepidoptera were obtained apart from *Cadra*. Although *C. cautella* has been recorded from Trinidad (Kaye & Lamont, 1927), this species was not found in the survey. Given the observations of Bondar (1940a, 1940b), it seems likely that further surveys will show that one or more *Cadra* spp. develop in palm inflorescences in Trinidad.

Of the moths reared, three could not be identified beyond family, three could only be identified to genus, and the remaining six were identified to species. These six comprise two species associated with coconut (*Atheloca bondari*, *Batrachedra nuciferae*) and four that are polyphagous and widespread (*Xystrologa nigrivitta*, *Anatrachyntis rileyi*, *Erechthias minuscula*, *Phidotricha erigens*). Of these, *P. erigens* has long been known from Trinidad (Kaye & Lamont, 1927), *B. nuciferae* was reported recently (MALMR, 2006, 2008), and *X. nigrivitta* was reported from Trinidad only after the survey was completed (Davis *et al.*, 2012). The remaining species (*Atheloca bondari*, *Anatrachyntis rileyi*, *E. minuscula* and the partially identified species) have not previously been reported from the island. This supports the suggestion of Cock (2003) that a large number of species from the families of smaller moths remain to be identified from Trinidad, and that surveys of specialist niches will rapidly generate new information on these.



Figure 8. Views of old male inflorescence of *Attalea maripa*, from Bush Bush Island showing Lepidoptera frass, and stamen remains held together with silk webbing.

Anatrachyntis rileyi and *E. minuscula* are considered to be of Old World origin and so must have been introduced with trade, probably long ago. *Batrachedra nuciferae* was suspected to be an introduced species spreading in South America (MALMR, 2006, 2008), but Cock (2013) suggests it is more likely to be an indigenous species that has been overlooked. The remaining species, including those only identified to genus and family are likely to be indigenous species, not previously reported.

Some of the moths appear to be specialists associated with particular palm species, while others are generalists. Those thought to feed on living tissue (*Atheloca bondari*, *Batrachedra* spp.) are relatively specialised on two species. Those thought to be detritivores appear to be a mixture of specialists (*X. nigrivitta* on *Roystonea oleracea*,

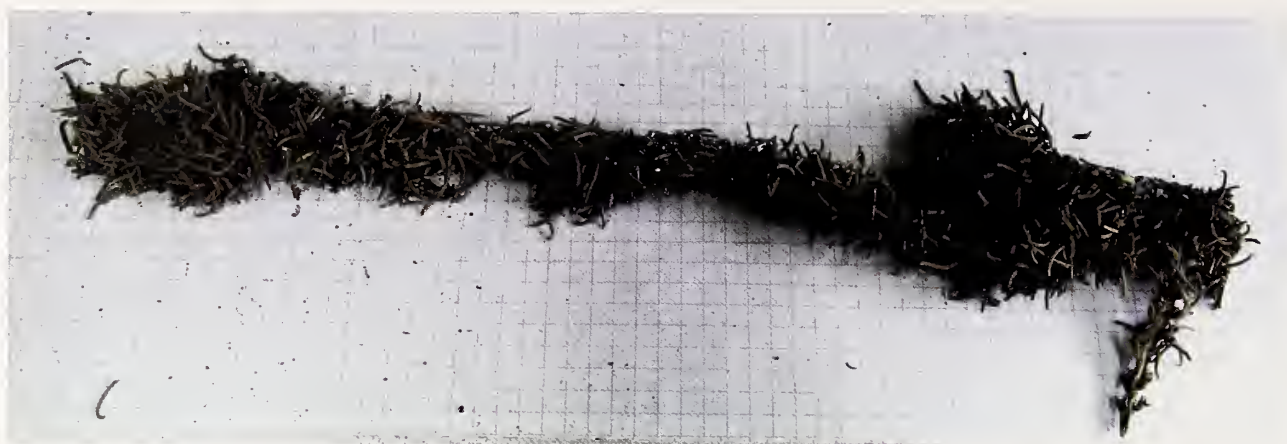


Figure 9. Half of the 'tunnel' made by an unidentified Lepidoptera species found amongst the old male inflorescence of cocorite, *Attalea maripa*, Bush Bush Island. Scale squares = 4mm.

unidentified Gelechiidae species and unidentified Cosmopterigidae sp. 1 on *Attalea maripa*, unidentified Cosmopterigidae sp. 2 on *Mauritia flexuosa*) and generalists (*Holcocera* sp., *Anatrachyntis rileyi*, and *E. minuscula*, each on several palms). However, *X. nigrivitta* has been reared from a bracket fungus (Davis *et al.*, 2012), so it is not a specialist as this survey suggested, and this also may prove to be the case when more is known about the three unidentified species.

There were three different patterns for the delay of emergence of moths from the collection date for the samples (Fig. 1). *Atheloca bondari*, the two *Batrachedra* spp. and unidentified Cosmopterigidae sp. 2 (from old *M. flexuosa*) all emerged within the first month; the unidentified Gelechiidae species, unidentified Cosmopterigidae sp. 2 and *Neodavisia* sp. (all from dead *Attalea maripa*) emerged at a fairly steady, low rate over two months; and *Holcocera* sp., *X. nigrivitta*, *Anatrachyntis rileyi*, and *E. minuscula* emerged primarily in the second month after the emergence boxes were set up. We suggest these patterns represent two different life styles. The first group, those species feeding on fresh plant material, rapidly completed their development and emerged within a month, whereas the last group, developing as detritivores, completed their development more slowly, either because they started later or because the poorer food quality dictated slower development, and emerged after the plant-feeding species. The middle group also are detritivores, reared from dead inflorescences of *Attalea maripa* and *M. flexuosa*, but because the sample of inflorescence was already dead, the moths had completed development and started to emerge immediately after collection.

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BOOK REVIEW

Flight Behavior by Barbara Kingsolver, 2012

Harper, New York. Hardbound, 437 pp. ISBN 978-0-06-212426-5. Price: \$28.99. Also available from Harper Audio and Harper Collins e-Books.

Most generous “Butterflies of...” reviews conclude with “this book should be on your bookshelves.” Rarely do we review novels in a scholarly scientific journal, but this is a truly remarkable and insightful work that should be read by all lepidopterists and certainly conservation biologists. Overriding the tense familial relationships that form the human interest core of a novel, which may be viewed as a soap opera by many biologists, there are layers of factual and hypothetical data that are true, and well supported extrapolations that address the most serious, yet largely avoided, problems of our world. Add in Kingsolver’s simple and compelling treatment of scientific thought processes. Brilliant. Anyone in education may pick up neat approaches here, as the situation distinguishing correlation and causation goes down like the spoon full of sugar.

To me the grandest concept is the reasoning of why the vast majority of the general population, including too many leaders, is negative towards science and scientists. This lack of communication seems the ultimate cause of the coming environmental collapse by global warming. The plot unfolds with two major characters, a smart uneducated young woman, Dellarobia Turnbow, and a bright and cynical early middle age professor, Ovid Byron, weaving significant sets of discussion following Dellarobia’s discovery of a rogue colony of Monarch butterflies on her small farm in Appalachia Tennessee. The appearance of the Monarchs is consequent to the extinction of the

Mexican montane migratory population. Needless to say the presentation of the entire Monarch story is outstanding through the devise of Dellarobia serving as an assistant to Byron and learning techniques of data collecting and interpretation. Kingsolver, in addition to an education and work experience in Biology, had input from Lincoln Brower and other players in both butterfly biology and contemporary conservation. There does not appear to be a single error in the book. Most stunning is the readability in spite of some tedious stalls in the family stress parts of the tale.

The setting in a “red neck” fundamentalist Tennessee economically marginal community is perfect, plus the habitat provided is plausible to the story. The human population represents the common man, whose variety and behavior represent everywhere. Unfortunately time is running out on influencing the environmental changes already entrained. The latest information indicates the Mexican Monarch populations are now in their final years. And few really care if they even know. The tragedy of losing the Monarch Migration Phenomenon is more than sad, it advertises loud and clear there is no turning back until it will be too late. Nobody wants to hear this. Monsanto does not wish to lose its Roundup profits, etc. Do not fail to read this book.

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New and revised descriptions of the immature stages of some butterflies in Sri Lanka and their larval food plants (Lepidoptera: Lycaenidae). Part 1: Polyommatainae and Theclinae, in part.

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Abstract. The immature stages of 24 of the 84 species of butterflies of the family Lycaenidae (Polyommatainae and Theclinae, in part) in Sri Lanka are described. The immature stages of 11 species are reported for the first time (including 4 endemic species, 2 endemic subspecies, plus 2 species and 1 subspecies restricted to Sri Lanka and India). Larval food plants of 23 species in Sri Lanka are documented for the first time while for 6 species larval food plants previously reported in Sri Lanka are confirmed. The immature stages of 7 species that have been previously described from Sri Lankan material and 5 species described from Indian material are compared to the findings of the current study and additional observations are presented. This study provides basic information for further studies on the biology of these species which will also be relevant for conservation of butterflies in Sri Lanka.

Keywords: Immature stages, larval food plants, ant association, Sri Lanka, Ceylon, Lycaenidae, Polyommatainae, Theclinae, butterflies, conservation.

INTRODUCTION

A comparison of the latest National Red List data (van der Poorten, 2012) on the butterfly fauna of Sri Lanka to historical records (e.g. Ormiston, 1924; Woodhouse, 1949) suggests that the populations of many of the 245 species known in the country have declined. The National Red List 2012 lists 21 species as CR (critically endangered), 38 as EN (endangered), 40 as VU (vulnerable), 20 as NT (near threatened) and 6 as DD (data deficient). As with many other countries, the loss of habitats along with larval food plants seems to be the main cause for these declines.

To address these declines, the Biodiversity Secretariat of the Ministry of Environment of Sri Lanka is developing a Butterfly Conservation Action Plan. However, in order to assess the status

of a butterfly species and to prepare conservation management plans, information on the bionomics of the species including the larval food plants and the resource needs of the adults as well as of the immature stages is a prerequisite.

However, the immature stages and larval food plants of the butterflies in Sri Lanka are incompletely known. Woodhouse (1949) published information on the immature stages and larval food plants of 191 of the 242 species of butterflies in the island known at that time. Of these descriptions, 80 were based on work done in Sri Lanka and 111 were based on work done in peninsular India. Little research has been published since then (but see van der Poorten & van der Poorten, 2011).

Knowledge of immature stages and larval food plants, as well as being important for conservation of butterflies, is also useful in classification, elucidating broad-scale evolutionary patterns, understanding ecology at the community and population levels, and in ecological chemistry (DeVries, 1986 and references therein). Knowledge of the immature stages is also important at a more practical level since it enables the identification of larvae and pupae in the field, which can increase the accuracy of surveys even in the absence of adults. Additionally this knowledge is valuable in aiding the development of ecotourism (e.g. establishment of butterfly parks,

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butterfly watching) which is an important economic activity for a country such as Sri Lanka.

In the current study (conducted from 2004 to the present and ongoing), we have documented the immature stages and larval food plants of 176 of the 245 known species of butterflies in Sri Lanka. For more details on the background and approach, see van der Poorten & van der Poorten (2011).

There are 84 species in the family Lycaenidae in Sri Lanka in 4 subfamilies – Curetinae (1 species), Miletinae (1 species), Polyommatainae (1 tribe, 48 species), and Theclinae (11 tribes, 34 species). In this paper, we present the immature stages and larval food plants in Sri Lanka of 15 of the 48 species of Polyommatainae (8 for the first time; genera *Chilades*, *Jamides*, *Nacaduba*, *Prosotas* and *Tarucus*) and 8 of the 34 species of Theclinae (3 for the first time; genera *Arhopala*, *Surendra*, *Hypolycaena*, *Pratapa* and *Tajuria*). Other Lycaenidae will be discussed in subsequent papers.

The immature stages of 7 species covered here have been previously described from Sri Lanka material though most of the descriptions are very brief and only refer to the final larval instar and the pupa. An additional 5 species (not necessarily the same subspecies) have been described from India. These older descriptions are compared to the findings of the current study and additional observations are presented.

For 23 species, new larval food plants are reported for the first time (and additionally for one species for which there is no description available of the larva or pupa), while for 6 species larval food plants previously reported in Sri Lanka are confirmed.

For the majority of lycaenid species worldwide whose life histories have been recorded, ant-larval associations ('myrmecophily') are documented. These associations may be mutualistic or parasitic, and facultative or obligate. Some species of Lycaenids associate loosely with several species of ants (facultative myrmecophiles) while others are more closely tied to an association with only one or perhaps two ant species (obligate myrmecophiles) (Fiedler, 1991; Pierce *et al.*, 2002).

MATERIALS AND METHODS

For rearing methods, see van der Poorten & van der Poorten (2011). Plants were identified to species if possible, using several references (most notably, the series edited by Dassanayake (1980-1998)) and an inspection of herbarium specimens at the Herbarium of the Royal Botanic Garden in Peradeniya, Sri Lanka. No voucher specimens were deposited. Nomenclature of butterflies follows K. Kunte (pers. comm.).

Where information on the duration of developmental stages is given, these data were obtained in rearings at ambient temperatures (22–34°C) at Bandarakeswatta (07.37.01N, 80.10.57E), 70 m asl, North Western Province, Sri Lanka. Conventions used (applied to both the larva and the pupa): Segments are numbered S1 to S14 (S1—the head; S2 to S4—the 3 segments of the thorax; S5 to S14—the 10 segments of the abdomen). In the photographs, the head is always on the left.

RESULTS AND DISCUSSION

Subfamily: Polyommatainae

Chilades parrhasius nila Evans, 1925. Small Cupid. Endemic subspecies.

In the current study, the immature stages of *C. parrhasius nila* in Sri Lanka are described and the larval food plant identified for the first time.

Notes on immature stages: Egg: dome-shaped, micropyle region depressed to form a concavity, fine surface protuberances forming hexagonal areas (Fig. 1a). 1st instar: head black, body pale yellowish-green. 2nd: not recorded. 3rd (Fig. 1b) & 4th (Fig. 1c): same as 5th. 5th: head black, ground color of body variable from 3rd–5th instars ranging from light green to dark red (each individual can change color from one instar to the next; color seems to be associated with the color of the leaves they eat (red or green)), dorsal band dark green to almost red (in some individuals both colors are present), subtended by a white band; white lateral, supraspiracular and dorso-ventral bands; yellow, brown or reddish between each set of white bands; S2 with depressed area dorsally; entire larva with numerous setae giving it a fuzzy appearance, S11 with dorsal nectar organ (DNO), S12 with a pair of eversible tentacles (TOs); banding highly variable (some lines may be absent or obscure) (Figs. 1d–f). In the field, larvae were attended by ants (species not identified) but they developed normally in the lab without them. Pupa: very similar to that of *C. pandava lanka* but more rounded; ground color variable from pale brownish-green to pale pinkish-green to pale yellow; some with darker brown bands with numerous small markings along the wing buds; abdomen mottled with dark brown and with three lines – a black dorsal discontinuous line and a lateral blotchy line; extent and color of markings variable. In the lab, larvae pupated among leaves (Figs. 1g–i). A dipteran parasitoid (species not identified) emerged from one pupa (Fig. 1j). Length (mm): prepupation (10); pupa (6–8). Duration of immature stages (days):

pupa (6–7); egg to emergence of adult (29–30). The immature stages illustrated by Bhakare (2012) of *C. p. parrhasius* in India are similar except that the pupa is whiter and less spotted.

Larval food plant: The current study showed that *Acacia eburnea* (H. D. Jayasinghe, pers. comm.) and *A. leucophloea* (Fabaceae: Mimosoideae) are larval food plants in Sri Lanka. The larva feeds only on tender leaves. *Acacia* has been reported for *C. p. parrhasius* in India (K. Kunte, pers. comm.) and additionally *Prosopis* in Saudi Arabia (Larsen, 1983).

C. parrhasius nila is found only in the arid and dry zones. *A. eburnea* is found only in the arid zone where it is very common; *A. leucophloea* is common in the arid, dry and intermediate zones (Dassanayake, 1980). At Yala National Park in the southeast, *C. parrhasius nila* feeds mostly on *A. eburnea* since *A. leucophloea* is uncommon there. In the arid zone of the northwest and the dry zone of the north, *C. parrhasius nila* commonly uses *A. leucophloea*. The distribution of these two larval food plants matches that of the butterfly in that at least one of these two larval food plants has been found wherever the butterfly has been recorded.

Chilades lajus lajus (Stoll, 1780). Lime Blue.

The immature stages of *C. l. lajus* in Sri Lanka have not been described. In India, de Nicéville (1890) briefly described the final instar larva and pupa of *C. lajus*. The findings of the current study agree with this description except that in the pupa, the ground color is highly variable (pale green to dark green) and the markings are variable (almost none to heavily blotched) (Figs. 2a–d). The final instar and pupa look similar to those illustrated in Igarashi & Fukuda (2000) from Bhutan (subspecies not identified).

Additional notes on immature stages: 4th instar (Fig. 2e); same as 5th (Fig. 2f). ADNO and TOs were noted in the 4th & 5th instars. The larvae were often gregarious and were found feeding in twos and threes. The larva was almost always attended in the field by ants (species not identified) but this was not obligatory; the larvae developed normally in the lab without ants. Duration of immature stages (days): pupa (5).

Larval food plant: In Sri Lanka, de Nicéville & Manders (1899) reported that the larva fed on *Citrus* and Woodhouse (1949) reported, without a reference, that it fed on “Rutaceae, *Limonia acidissima*, and various species of *Citrus*.” The current study showed for the first time that *Atalantia ceylanica* (S. Sanjeeva, pers. comm.), *Atalantia monophylla*, *Citrus aurantifolia* and *C. sinensis* are used as larval food plants in Sri Lanka and confirmed the use of *Limonia acidissima* (all Rutaceae). de Nicéville (1890) also reported species of *Citrus* as larval food plants in India, and Igarashi

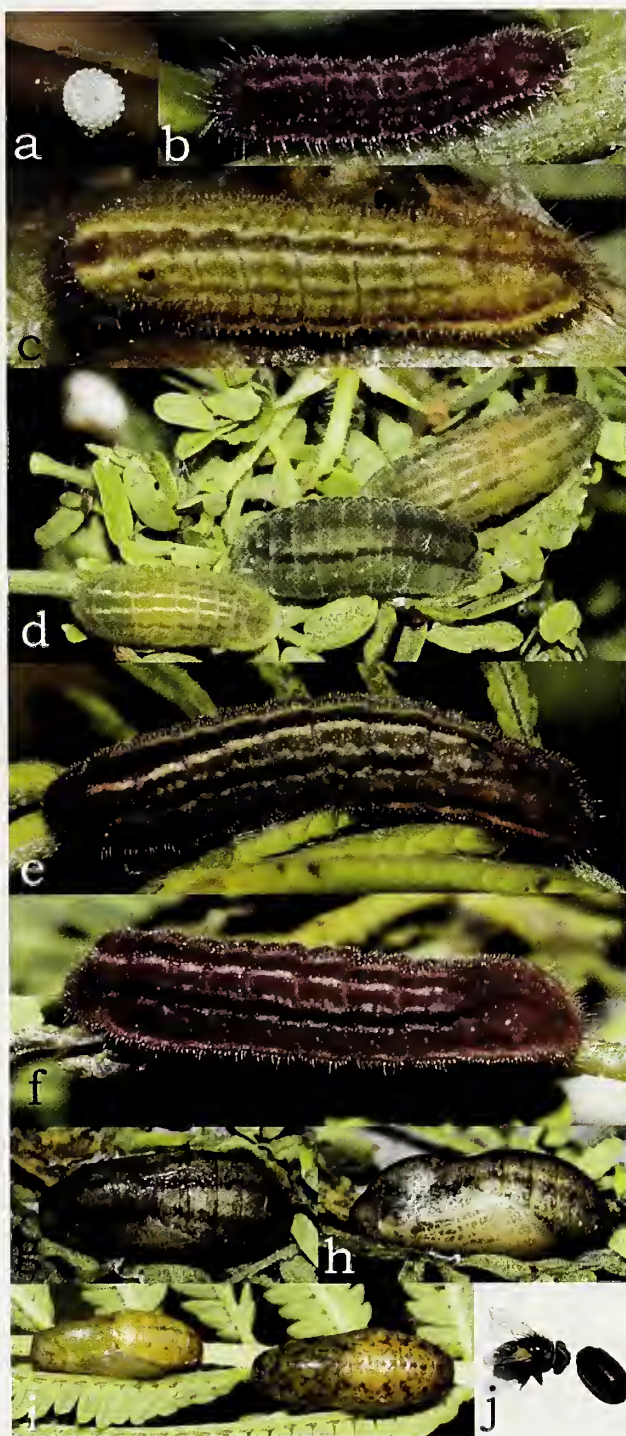


Figure 1. *Chilades parrhasius nila*. a. Egg. b. Larva, third instar, red form. c. Larva, fourth instar, green form. d. Larvae, fifth instar, green, dark green & red forms, green & red forms. e. Larva, fifth instar, dark red form. f. Larva, fifth instar, red form. g. Pupa, pale brownish-green form, dorso-lateral view. h. Pupa, pale brownish-green form, lateral view. i. Pupae, pale yellow form and pale pinkish-green form. j. Dipteran parasite with its pupal case



Figure 2. *Chilades lajus lajus*. a. Pupa, dark green form, heavily marked. b. Pupa, pale green form, lightly marked. c. Pupa, light green form, dorsal view. d. Pupa, as in (c), dorso-lateral view. e. Larva, fourth instar, attended by ants, lateral view. f. Larva, fifth instar, dorsal view

& Fukuda (2000) recorded members of the Rutaceae in India, Bhutan and Taiwan. Robinson *et al.* (2010) also lists Anacardiaceae and Tiliaceae from India but we have not been able to review these references. The early instar of the larva feeds on tender leaves; later instars feed on maturing leaves but not fully mature leaves.

Ch. l. lajus is widely distributed across the country but is particularly common in the dry and intermediate zones. *Limonia acidissima* is found mainly in the arid, dry and intermediate zones (both wild and cultivated), with some being planted in the wet zone. *Citrus aurantifolia* and *C. sinensis* are widely cultivated in the dry and intermediate zones and less commonly in the wet zone. *Atalantia ceylanica* and *Atalantia monophylla* are small native trees found widely distributed in the lowlands of all climatic zones. Even though at least one of these larval food plants has been found wherever the butterfly has been recorded, it is likely, given its propensity to feed on a wide range of plants, that other species of the family Rutaceae are also used as noted above.

Chilades pandava lanka (Evans, 1925). Plains Cupid. Endemic subspecies.

The final instar larva and pupa of *C. pandava lanka* were illustrated and described briefly by Moore (1880) from Sri Lankan material. In India, the larva and pupa of *C. pandava* were described by Davidson *et al.* (1896), de Nicéville (1890) and Bell (1918a). The findings of the current study agree with these descriptions except for the following: a) the fifth instar larva has two color forms – violet-brown and yellowish-green; other markings are as described by the earlier authors (Fig. 3a); b) the pupa also has an additional color form—violet brown without any green; both color forms are heavily blotched on the dorsal side of the abdomen and head (Figs. 3b–e).

Additional notes on immature stages: Egg: similar to that of *C. parthasius nila* (Fig. 3f). 1st instar: not recorded. 2nd: head black, body pale brown, distinct brown dorsal band and brown lateral band, a series of white markings on either side of dorsal line, S14 with a black dorsal patch, body covered with minute setae (Fig. 3g). 3rd: similar to 2nd but white markings more distinct and with similar white markings subdorsally and laterally, black patch on S14 absent, S2 with depressed black area dorsally; DNO and TOs visible (Fig. 3h). 4th: similar to the yellowish-green form of the 5th instar (Fig. 3i). The final instar and pupa are similar to those illustrated in Igarashi & Fukuda (2000) from Taiwan (subspecies not indicated) except that the Taiwan larvae appear more orangish overall. All instars were attended in the field by ants (species not identified) but they developed normally in the lab without ants (Figs. 3j, k). In the field, pupation took place at the base of the cataphylls, often underneath the debris of fallen leaves. Some pupae were also attended by ants.

Larval food plant: In Sri Lanka, Moore (1880) quoted from Thwaites who said it fed on “Cycadaceae”; de Nicéville & Manders (1899) reported that it fed on “young fronds of cycads”; and Manders (1904) reported that larvae were collected from “a species of *Cycas* on the [Colombo National] Museum lawn”. Igarashi & Fukuda (2000) also reported it feeding on a *Cycas* (*Cy. revoluta* in Taiwan). There are also records of it feeding on members of the Fabaceae (e.g. *Xylia dolabriformis* in India (Bell, 1918a)). The current study showed the precise species identity of locally used larval food plants as *Cycas nathorstii* and *Cy. revoluta* (Cycadaceae). The larva feeds on tender leaves but when this supply runs out, it feeds on the undersurface of maturing leaves leaving the upper epidermis intact. It does not feed on mature leaves. The eggs are laid singly but since they are laid in large numbers on each leaf frond, the new flush of leaves is sometimes completely consumed by a brood. We have not observed it feeding on any Fabaceae.

Ch. pandava lanka is widely distributed in all climatic zones. *Cycas nathorstii* is widely distributed in forested areas of all the climatic zones including Wilpattu National Park, Bibile, Nilgala and Gampaha (Lindström & Hill, 2002; Lindström & Hill, 2007).

Cy. revoluta is a cultivated plant that is widely planted in gardens. The distributions of *Cy. nathorstii* and *Cy. revoluta* fit that of the butterfly in that at least one of these two plants has been found wherever the butterfly has been recorded. Since there is only one other species of *Cycas* in Sri Lanka that is very rare, it is unlikely that the butterfly has another larval food plant.

Jamides bochus bochus (Stoll, 1782). Dark Cerulean.

The egg, first instar and final instar larva of *J. b. bochus* were described by Green (1905) from Sri Lankan material. In India, Davidson *et al.* (1896) briefly described the final instar larva of *J. bochus* and reported that the pupa was indistinguishable from that of *Chilades pandava* while Bell (1918a) described the final instar larva and pupa in detail. The results of the current study agree with Green including the manner of oviposition (eggs are deposited into a frothy mass exuded by the female) (Fig. 4a). They also agree with the descriptions of the final instar by these three authors though color variations were noted: ground color ranges from light green with faint darker green bands to reddish-brown with dark brown lateral and dorsal bands to purplish-brown with similar banding (Figs. 4b-d). Though Green said that he did not notice a “dorsal gland” (DNO) on S11, this organ and TOs are visible (Fig. 4e) from at least the 4th instar. The larva is occasionally attended by various species of ants (species not identified). Bell’s description of the pupa agrees with the results of this study (Fig. 4f). The larva and pupa illustrated in Igarashi & Fukuda (1997) from Taiwan are also similar.

Additional notes on immature stages: The larvae were occasionally found in very large numbers. In the lab, they developed normally without ants. Duration of immature stages (days): pupation (2); pupa (7–9); egg to emergence of adult (27–30).

Larval food plants: In Sri Lanka, Green (1905) reported that the larvae fed “on the anthers” and “on the flower buds of a species of *Vigna*.” Woodhouse (1949) reported “pods of Leguminosae”, and that it was “a pest of *Boga medelloa* (*Tephrosia candida*) when grown for green manure in Ceylon.” The current study showed for the first time that the following are larval food plants in Sri Lanka: *Derris scandens*, *D. elliptica*, *Pongamia pinnata*, *Tephrosia vogelii*, *Vigna radiata*, *V. unguiculata*, *Acacia auriculiformis*, *Cajanus cajan*, *Gliricidia sepium*, *Pueraria phaseoloides* and *Pterocarpus indicus* (Fabaceae). The current study confirmed that *Tephrosia candida* (Fabaceae) is a larval food plant in Sri Lanka. The larva feeds on flowers, especially the ovary and anthers, but did not eat tender leaves that we offered. Many species of Fabaceae have been reported as larval food plants of *J. bochus* from other countries as well, e.g. Japan (Igarashi & Fukuda, 1997) and Singapore (Butterfly Circle, 2012).

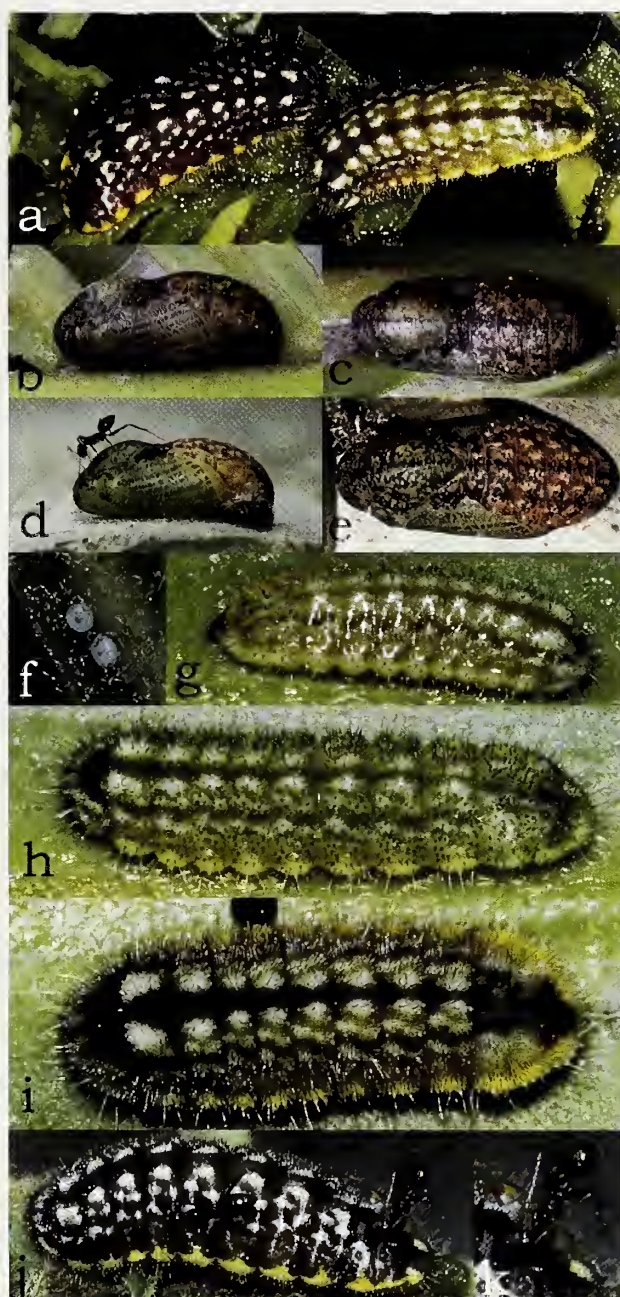


Figure 3. *Chilades pandava lanka*. a. Larva, Fifth instar, violet-brown form and yellowish-green form. b. Pupa, violet-brown form, lateral view. c. Pupa, violet-brown form, dorsal view. d. Pupa, green form, lateral view. e. Pupa, green form, dorsal view. f. Eggs. g. Larva, second instar. h. Larva, third instar. i. Larva, fourth instar. j. Larva, attended by ants. k. Close up of ant drinking from DNO.

J. b. bochus is common and widespread in Sri Lanka. The native larval food plants (*Derris scandens* and *Pongamia pinnata*) are widely distributed in the dry and intermediate zones and the hills. The other



Figure 4. *Jamides bochus bochus*. a. Egg mass. b. Larva, final instar, light pink, cream and green form. c. Larva, final instar, reddish form. d. Larva, final instar, purplish form. e. DNO. f. Pupa, lateral view

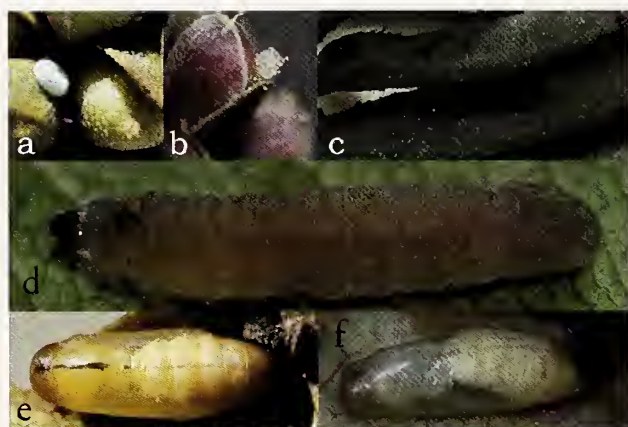


Figure 5. *Jamides coruscans*. a. Egg. b. Frass at entrance hole of larva. c. Larva, third instar. d. Larva, final instar. e. Pupa, dorsal view. f. Pupa, dorso-lateral view.

larval food plants are widely cultivated and *J. b. bochus* is occasionally a pest, particularly of *Cajanus cajan*. *G. sepium*, though an introduced, widely planted exotic, is heavily used in February and March before the onset of the mass migrations of this species. The distributions of the larval food plants reported here fit the distribution of the butterfly in that at least one of these larval food plants has been found wherever the butterfly has been recorded. However, since it is polyphagous, it is likely that other members of the Fabaceae are also used.

Jamides coruscans (Moore, 1877). Ceylon Cerulean. Endemic.

In the current study, the immature stages are described and the larval food plant identified for the first time.

Eggs: laid singly on flower buds or on young shoots when flower buds were unavailable, flattened disc with ridges and a circular depression at the micropyle region (Fig. 5a). 1st instar: the newly hatched larva bored into an unopened flower bud and fed on its contents. It threw its frass out of the entrance hole, leaving signs of its entry (Fig. 5b). It is pale yellowish-pink with a brown head. 2nd: not recorded. 3rd: S2 with a black diamond shaped dorsal patch posteriorly (Fig. 5c). 4th: not recorded. 5th: head brown, mouth parts and the lower half of the face darker brown, body pale brownish-pink with a frosted appearance because of numerous fine setae, faint darker pink dorsal line, spiracles brown, DNO and TOs present (Fig. 5d). Larger larvae exited the flower bud and hid in the inflorescence where it was well-camouflaged. The larva also fed on the very tender leaves of new flushes. All instars were sluggish and later instars hid under the large bracts that envelope the smaller twigs of the tree. Some larvae were accompanied by a small number of ants (species not identified) that were attracted by the DNO. Pupa: pale yellowish-pink to yellowish-brown, sometimes with a dark brown dorsal line on S2–S4 and a faint dorsal line to the end of the abdomen and with a dorsal spot on the last segment (Figs. 5e, f). In the lab, the larva pupated on the underside of a leaf. In the field, pupation presumably occurs on the tree, probably inside the large leaf bracts. Duration of immature stages (days): pupa (12).

Larval food plants: The current study showed that *Humboldtia laurifolia* (Fabaceae) is a larval food plant in Sri Lanka. All instars feed on tender leaves. The early instars also feed on unopened flower buds.

J. coruscans is found in the wet lowlands where it is fairly common along riparian habitats. *H. laurifolia* is an endemic tree that is widely distributed in the wet lowlands (Dassanayake, 1991). Its distribution matches that of *J. coruscans* (i.e. the plant has been found wherever the butterfly has been recorded).

Jamides celeno tissama (Fruhstorfer, 1916). Common Cerulean. Endemic subspecies.

The final instar larva and pupa of *J. celeno tissama* were described briefly by Moore (1880) from Sri Lankan material. In India, the final instar larva and pupa of *J. celeno* (as *Lampides aelianus*) were described by de Nicéville (1890) and Bell (1918a), all later quoted by Woodhouse (1949). The findings of the current study agree with these authors except for the following: a) we encountered only the green form, some with reddish markings (Figs. 6a, b); and b) the pupa is light brown with a tinge of purple (de Nicéville reported pale ochreous green) and it has



Figure 6 *Jamides celeno tissama*. a. Larva, final instar, green form, dorsal view. b. Larva, final instar, green form with red, dorsal view. c. Pupa, dorso-lateral view. d. Pupa, dorsal view. e. Larvae, third instar with DNO, TOs. f. Parasitoid wasp.

black markings (Bell reported brown markings) (Figs. 6c, d). TOs and a DNO were visible from the 3rd instar (Fig. 6e).

Additional notes on immature stages: The larva was sometimes attended in the field by ants (species not identified) but developed normally in the lab without them. When feeding on flowers, it bored into the flower. Larvae were sometimes parasitized by a parasitoid wasp (species not identified) (Fig. 6f).

Larval food plants: In Sri Lanka, Woodhouse (1949) recorded that the larva fed on flowers or young leaves of “*Pongamia glabra* [now *P. pinnata*], *Abrus precatorius*, *Butea frondosa* [now *B. monosperma*], *Saraca indica*”. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Vigna unguiculata* and *Pueraria phaseoloides*. The larva feeds on the flowers of these two species. The current study confirmed the use of *Pongamia pinnata* (young leaves) and *Abrus precatorius* (flowers and young leaves). All are species of Fabaceae. We were unable to confirm the use of *B. monosperma* and *S. indica* though both species are present in Sri Lanka. Larval affiliation with various species of Fabaceae is also reported from many other countries, e.g. Taiwan, India and the Philippines (Igarashi & Fukuda, 1997). Veenakumari *et al.* (1997) reported Marantaceae from the Andamans and Nicobar Islands, and Sapindaceae and Meliaceae are also noted in the literature (Eliot 1992).

J. celeno tissama is widely distributed over the island at all elevations. In the lower elevations, *Pongamia pinnata*, *Abrus precatorius* and *Pueraria phaseoloides* are the most commonly used larval food plants. In the mid-elevations, *Pongamia pinnata* and *Pueraria phaseoloides* are used. The larval food plant in the highest elevations is unknown. It is likely that several other species of Fabaceae or some other family are also used.

Jamides lacteata (de Nicéville, 1895). Milky Cerulean. Endemic.

In the current study, the immature stages (fifth instar larva and pupa) are described and the larval food plant identified for the first time.

Notes on immature stages: Final instar: head black and hidden, body usual lycaenid form, ground color brownish-pink to pink covered with minute black and white setae, posterior end of S2 with black dorsal patch (shaped like a blunt arrowhead), DNO on S11, a pair of subdorsal eversible tentacles on S12, S3–S14 with alternating dark- and light-colored oblique lines, S3–S10 with small dark bluish-gray patches dorsally (each patch studded with black setae) and zigzag lateral banding with a bluish tint, spiracles brown, S11–S14 with dark purplish-brown dorsal patch (Fig. 7a). Pupa: ground color light-pinkish brown, heavily mottled with dark brown and black, head, thorax and abdomen rounded dorsally, black markings confined to the dorsal and subdorsal lines, spiracles white (Figs. 7b, c). We did not observe ants in attendance.

Larval food plant: The current study showed that *Lepisanthes erecta* (Sapindaceae) is a larval food plant in Sri Lanka. The larva feeds only on tender leaves. Although most members of the genus *Jamides* use Zingiberaceae and Fabaceae as larval food plants, *J. lacteata*, like *J. aleuas* in Australia (Braby, 2000), belong to the small minority that use Sapindaceae.

J. lacteata is found in the forests of the intermediate and wet zones below about 800 m asl where it is uncommon. *L. erecta* is uncommon in forests of the moist low country to 1000 m asl (Dassanayake, 1998) and is scattered in the intermediate zone of the southeast. Its distribution appears to match that of

the butterfly. However, since *L. erecta* has not been recorded from all the locations that the butterfly has been recorded, it is possible that there is another larval food plant.

Jamides alecto meilichius (Fruhstorfer, 1916). Metallic Cerulean. Endemic subspecies.

The final instar larva and pupa of *J. alecto meilichius* were described briefly by E. E. Green from Sri Lankan material (quoted in de Nicéville (1890) as *Lampides elpis*). In India, the larva and pupa of *J. alecto* were briefly described by Davidson *et al.* (1896). Woodhouse (1949) quoted from these two sources. The current study agrees with Green's account except for the following points: a) the ground color of the larva is variable and seems to depend on the color of the larval food source – we encountered pale straw-colored larvae and reddish larvae (Figs. 8a, b) but not dull pale green ones; b) in the larva, DNO on S11 and TOs present on S12; and c) most pupae have 2 lateral black spots on S2 at the base of the wings and 2 well-defined subdorsal black spots on S4 just above the wings (Figs. 8c, d).

Additional notes on immature stages: Eggs were laid on the inflorescence of the plant (Fig. 8e). When *Amomum fulviceps* or *A. trichostachyum* is used, most eggs were laid on the top of the inflorescence (which is borne at ground level) since the lower half is frequently covered by fallen leaves. Despite this obstruction, the ♀ navigated through the fallen leaves to lay its eggs successfully, presumably by using olfactory cues. Though many eggs were frequently seen on a single inflorescence, there were never more than two larvae. The larva fed mostly on the large anthers of the flowers by boring into the flower bud; it expelled its frass to the outside (Fig. 8f). Larger buds were preferred, and open flowers were not used despite easy access and visibly large anthers. When the floral bracts were pulled out and the larva exposed, it hurriedly crawled back into the tightly clustered flowers and flower buds to hide. Under field conditions, the droppings were difficult to discern due to the multitude of rotting vegetation around the inflorescences, the frequent rain that washes away the droppings and the very wet conditions around the plant. One specimen in an early instar had white spiracles (Fig. 8g). Pupation occurred within the inflorescence, just inside a bract, with the head pointing up. Duration of immature stages (days): pupa (10–12).

Larval food plants: In Sri Lanka, Green (quoted in de Nicéville, 1890) recorded that the larva fed on the fruit of *Elettaria cardamomum*. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Alpinia purpurata*, *A. calcarata*, *Hedychiium flavescens*, *Zingiber zerumbet* and *Z. wightianum* (S. Sanjeeva, pers. comm.), *Z. cylindricum* (H. D. Jayasinghe, pers. comm.) and *Amomum fulviceps* and *A. trichostachyum*. The larva feeds on the flowers and young fruits of these plants. The current study also confirmed the use of the fruits of *Elettaria cardamomum* (S. Sanjeeva, pers. comm.) as a larval food plant. *J. alecto meilichius* does not appear to be a regular pest in cardamom plantations although



Figure 7. *Jamides tacteata*. a. Larva, final instar. b. Pupa, lateral view. c. Pupa, dorsal view



Figure 8. *Jamides alecto meilichius*. a. Larva, final instar, pink. b. Larva, final instar, straw-colored. c. Pupa, dorsolateral view. d. Pupa, dorsal view. e. Egg. f. Larva, hind end projecting from hole in flower bud with frass. g. Larva, early instar with white spiracles.

Woodhouse (1949) reported otherwise. All larval food plants are members of the Zingiberaceae. The use of Zingiberaceae by *J. alecto* has been recorded elsewhere as well, e.g. in India, the Andamans and Nicobar Islands or Singapore (Igarashi & Fukuda, 1997; Veenakumari *et al.*, 1997; Tan & Khew, 2012).

J. alecto meilichius is widely distributed but not common within the wet zone forests and wetter areas of the intermediate zone from sea level to about 800 m asl. *Alpinia purpurata*, *Zingiber zerumbet* and *Elettaria cardamomum* are cultivated plants in the wet zone. The other larval food plants are native plants that are found in the forests of the intermediate and wet zones (Dassanayake, 1983). Though the distribution

of the known larval food plants matches that of *J. alecto meilichius* in that at least one of these larval food plants has been found wherever the butterfly has been recorded, it is very likely that other species of Zingiberaceae are also used.

Nacaduba hermus sidoma Fruhstorfer, 1916. Pale Four Lineblue.

The immature stages and larval food plant of *N. hermus sidoma* have not been described in Sri Lanka or in India, the only two countries in which this subspecies occurs. In the current study, the immature stages (fifth instar and pupa) are described and the larval food plant identified for the first time.

Notes on immature stages: Final instar: head light brown, ground color greenish-white to pink, pink forms with greenish-white hue on S5–S10 and faint dorsal line of a darker pink from S3–S11, posterior end of S2 with rhomboidal shaped dorsal patch which is whitish on the pink form and green on the green form, segments deeply furrowed and clearly marked except S11–S14, DNO on S11, pair of eversible tentacles on S12, anterior edge of S5–S10 with darker, slightly depressed dorsal spot (Figs. 9a–d). Ants (species not identified) were seen feeding on the DNO of the larva but in the lab, the larva developed normally without them. Pupa: light brown to reddish brown, heavily speckled with small black markings, speckling heavier on dorsal line, a large black subdorsal mark on S4–S5, similar patch on S2, spiracles pinkish or white (Figs. 9e, f).

Larval food plant: The current study showed that *Symplocos cochinchinensis* (Symplocaceae) is a larval food plant in Sri Lanka. The larva feeds only on tender leaves. *N. hermus swatipa* in Koh Samui Island (Thailand) has been recorded feeding on the flowers of *Embelia subcoriacea* (Myrsinaceae), *Nephelium lappaceum* (Sapindaceae) and *Waltheria indica* (Sterculiaceae) (Day, 2012).

N. hermus sidoma is a seasonally common species of the wet zone. *Symplocos cochinchinensis* is a common shrub or tree found mostly in the wet zone from sea level to 2100 m asl (Dassanayake, 1981b). The distribution of *S. cochinchinensis* matches that of *N. hermus sidoma* in that the plant is found wherever the butterfly has been recorded but there are many other species of *Symplocos* growing alongside *S. cochinchinensis* and it is likely that some of these species may also be used.

Nacaduba sinhala Ormiston, 1924. Pale Ceylon Six Lineblue. Endemic.

In the current study, the immature stages are described and the larval food plant identified for the first time. There has been some confusion over the



Figure 9. *Nacaduba hermus sidoma*. a. Larva, final instar, pink form, lateral view. b. Larva, final instar, pink form, dorsal view. c. Larva, final instar, green form. d. Larva, final instar, light pink form. e. Pupa, lateral view. f. Pupa, dorsal view.



Figure 10. *Nacaduba sinhala*. a. Larva, final instar, with ant, dorsal view. b. Larva, final instar, dorso-lateral view. c. Pupa, dorsal view.

identity of this species. Woodhouse (1949) equated it with *N. atrata* Moore and quoted the description of the larva and pupa from Davidson *et al.* (1896) and Bell (1918b). He further listed the larval food plants as “*Embelia robusta*, *E. ribes* and *Ardisia humilis*” without any reference, though he apparently quoted from Bell (1918b) reporting on *N. atrata* [now *N. beroe*]. Neither description nor larval food plant applies to *N. sinhala*.

Notes on immature stages: 3rd instar: similar to final instar but more slender, white markings less apparent, S5–S12 with white dorsal spot. Final instar: ground color pale to bright reddish-pink, S11 with

DNO, S12 with eversible tentacles, S1–S11 clearly demarcated, S12–S14 obscurely demarcated, S3–S10 with whitish or yellowish subdorsal band, similar band along the spiracular line, body covered with minute setae which give it a frosted appearance, spiracles white, S3–S10 with slight transverse furrow in middle, posterior margin of S2 with a light pink diamond shaped dorsal spot, S11–S14 with dark purplish tinge. In the field, the larva was attended by ants (species not identified) but in the lab it developed normally without them (Figs. 10a, b). Pupa: dark reddish brown speckled with black, 2 large black rhomboidal subdorsal marks on S4 and S5 bordering the wing, similar black patches at base of wings (Fig. 10c).

Larval food plant: The current study showed that *Dimocarpus longan* (Sapindaceae) is a larval food plant in Sri Lanka. The larva feeds only on tender leaves. There are no records of the larva feeding on the cultivated form of *D. longan*.

N. sinhalensis is common in the intermediate zone and the Uva province. *Dimocarpus longan* is common in forests of the dry, intermediate and wet zones from sea level to 700 m asl (Dassanayake, 1998). Its distribution matches that of *N. sinhalensis* in that the plant has been found wherever the butterfly has been recorded and it is likely that it is the only larval food plant.

Nacaduba berenice ormistoni Toxopeus, 1927.

Rounded Six Lineblue.

The immature stages and larval food plant of *N. berenice ormistoni* in Sri Lanka have not been described. In India, the larva and pupa of *N. plumbeomicans* were described briefly by Davidson *et al.* (1986) and in detail by Bell (1918b) though it is not clear if these descriptions refer to *N. berenice ormistoni* which is also found in India in the Western Ghats. In the current study, the immature stages are described and the larval food plant identified for the first time.

Notes on immature stages: Final instar: ground color pink to various shades of light green, S3–S11 with 2–3 oblique rather indistinct white lateral lines, head pale brown, dorsal line darker but similar to ground color, S11 with DNO, S12 with a pair of eversible tentacles, body covered with fine white setae but in the green form, some individuals have dark brown setae (Figs. 11a–f). Pupa: head and thorax pinkish-brown, wings yellowish-brown, abdomen light pink, entire body heavily speckled with black, markings on dorsum form an irregular black line, S4–S5 with two distinct subdorsal black patches and one at wing base, spiracles black, some individuals lighter colored (Figs. 11g–i).

Larval food plant: The current study showed that *Lepisanthes tetraphylla* (Sapindaceae) is a larval

food plant in Sri Lanka. The larva feeds on tender leaves, flowers and flower buds. In other countries, *N. berenice* is recorded as feeding on a wide variety of plants. For example, Braby (2000) reported the families Proteaceae, Ulmaceae and Sapindaceae while Parsons (1999) additionally reported Fabaceae-Mimosoideae.

N. berenice ormistoni is not commonly reported in Sri Lanka but is widely distributed in the wet and intermediate zones—current reports include Matara, Galle, Haldumulla, Deniyaya, Badulla and Bandarakoswatta near Wariyapola. *Lepisanthes tetraphylla* is common in the forests of the dry and intermediate zone but rare in the forests of the wet zone (Dassanayake, 1998). It is possible that *N. berenice ormistoni* feeds on a different plant in the wet zone, possibly *L. erecta*.

The immature stages and larval food plants of the other *Nacaduba* species in Sri Lanka have not yet been described and in the course of this study, immatures have not been found: *N. calauria evansi* Toxopeus, 1927 (Dark Ceylon Six Lineblue), *N. beroe minima* Toxopeus, 1927 (Opaque Six Lineblue, endemic subspecies), *N. ollyetti* Corbet, 1947 (Woodhouse's Four Lineblue, endemic) and *N. pactolus ceylonica* Fruhstorfer, 1916 (Large Four Lineblue, endemic subspecies). The final instar and pupa of *N. kurava prominens* (Moore, 1877) (Transparent Six Lineblue, endemic subspecies) were described by Moore (1880).

Prosotas nora ardates (Moore, [1875]). Common Lineblue.

The final instar larva and pupa of *P. nora ardates* in Sri Lanka has not been described. In India, Bell (1918b) described in detail the larva and pupa of *P. nora* (as *P. ardates*). Note: many earlier authors confused *P. noreia*, *P. nora* and *P. dubiosa*—it was commonly thought that *P. nora/ardates* had tailed and tailless forms and that *P. noreia* was the tailless form of *P. nora* (as *P. ardates*). It is now established that the tailed form is *P. nora ardates*; the tailless form that closely resembles *P. nora ardates* is *P. dubiosa indica*; and the other tailless form is *P. noreia* (easily distinguished by the white cilia at the apex of the forewing and by the basal band on the underside of the forewing being confined to the cell) (Wynter-Blyth, 1957). The results of the current study agree with the descriptions by Bell (1918a) except for the following: a) in the larva, on the posterior end of S2 there is a whitish dorsal patch, and the ground color is much more variable and ranges from light green to green to greenish-red to reddish-pink, the dorsal line is usually red but can be green, or red and green (Figs. 12a–e); one larva was almost entirely

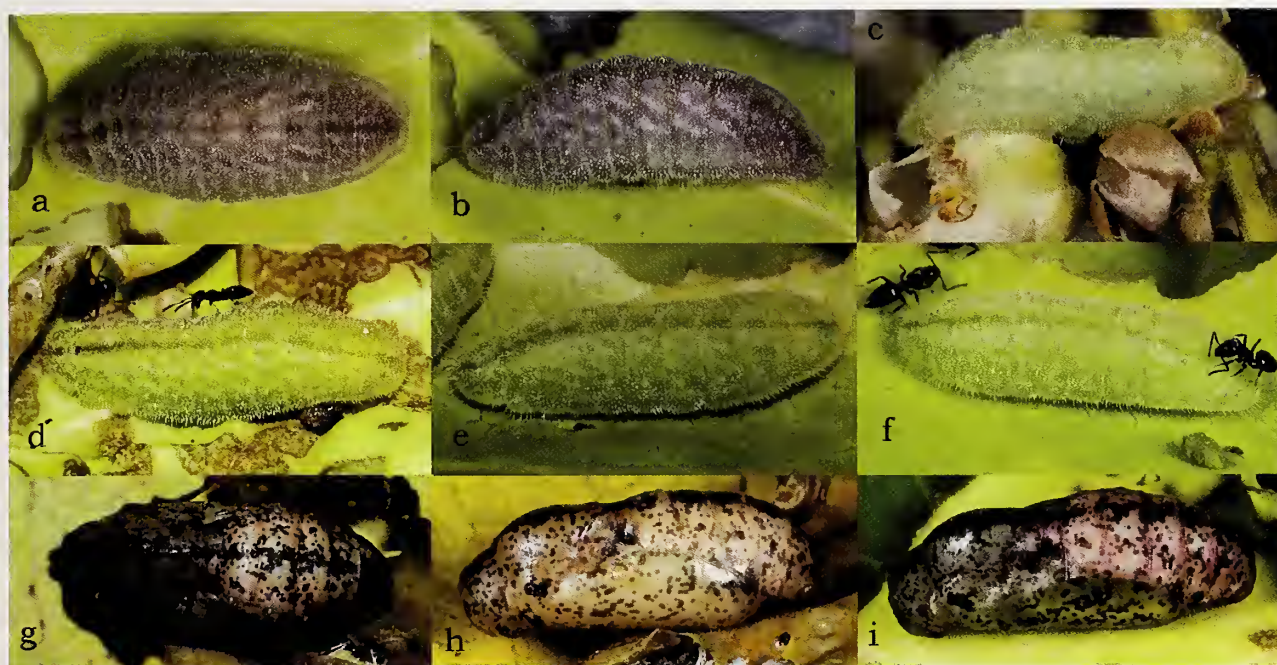


Figure 11. *Nacaduba berenice ormistoni*. **a.** Larva, final instar, pink form, dorsal view. **b.** Larva, final instar, pink form, dorso-lateral view. **c.** Larva, final instar, pale green form, feeding on flowers. **d.** Larva, final instar, green form with brown setae. **e.** Larva, final instar, green form with white setae. **f.** Larva, final instar, green form, with ants. **g.** Pupa, dark form. **h.** Pupa, light pink form. **i.** Pupa, pink form.

pale whitish-green with only a red interrupted dorsal line (Fig. 12f); DNO and TOs noted; b) in the pupa, only the abdomen is pinkish-brown—the head, thorax and wings are light greenish-brown and heavily speckled with dark markings (Figs. 12g, h) but in some pupae, the dorsum of the thorax is also pinkish-brown (Fig. 12i).

Additional notes on immature stages: In the field, the larvae were sometimes attended by ants (species not identified) but in the lab they developed normally without them.

Larval food plant: In Sri Lanka, Green (1912), writing under *Nacaduba ardates*, reported that “The larva of the tailed form has been bred by Mr. J. C. F. Fryer, from the flowers of *Allophylus* [sic] *cobbe*.” The current study showed for the first time that the following are larval food plants in Sri Lanka: *Croton aromaticus* (Euphorbiaceae) (S. Sanjeeva, pers. comm.), *Terminalia catappa* (Combretaceae) (S. Sanjeeva, pers. comm.), *Acacia caesia*, *A. pennata*, *Derris scandens*, *Pithecellobium dulce* and *Samanea saman* (Fabaceae). The larva feeds only on flowers. The current study also confirmed the use of flowers of *Allophylus cobbe* (Sapindaceae).

P. nora ardates is common and widely distributed over the island, in all climatic zones, from sea level to almost 2000 m asl. *Acacia caesia* is a native creeper that is widespread, found mainly in the dry zone but also in

the lower elevations of the wet and intermediate zones near water courses. *A. pennata* is a native that is found in the dry and intermediate zones only. *Pithecellobium dulce* is a small tree that has become naturalized in the dry and intermediate zones and is planted in urban landscapes in Colombo and along the southwest coast. *Samanea saman* is a large introduced tree that is widely planted across the country in all climatic zones (except the arid zone) up to about 600 m asl (Dassanayake, 1980). *Allophylus cobbe* is a native shrub that is widespread in all climatic zones though it is more common in the drier areas (Dassanayake, 1998). The distributions of these larval food plants match that of the butterfly except at its highest elevations (e.g. Nuwara Eliya) where it must be using a different larval food plant since none of these plants are found there. Robinson *et al.* (2010) report Myrtaceae, Sapindaceae and Combretaceae from other countries but we have not been able to review these references.

Prosotas dubiosa indica (Evans, [1925]). Tailless Lineblue.

The immature stages and larval food plant of *P. dubiosa indica* in Sri Lanka have not been described. See the note under *P. nora ardates*. In the current study, the final instar larva and pupa are described and the larval

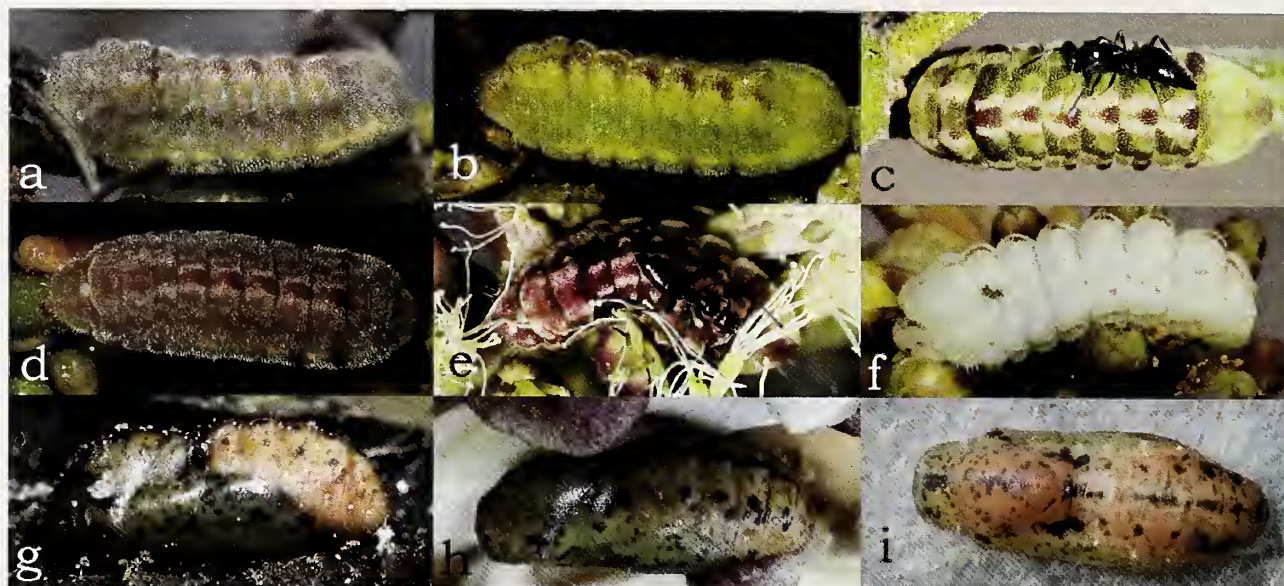


Figure 12. *Prosotas nora ardates*. a. Larva, final instar, pale green form. b. Larva, final instar, green form. c. Larva, final instar, dark green form. d. Larva, final instar, reddish form. e. Larva, final instar, red form. f. Larva, final instar, pale whitish-green form. g. Pupa, usual color form, lateral view. h. Pupa, usual color form, dorso-lateral view. i. Pupa, with pink dorsum of thorax, dorsal view.

food plant identified in Sri Lanka for the first time.

Notes on immature stages: Final instar larva: head light brown, ground color of body pale green, shape same as *P. nora ardates*, dark green dorsal band with minute red markings from S3–S14, diffuse greenish-whitish subdorsal band from S4–S10, broad white dorso-ventral band from S3–S14, spiracles white, DNO and TOs present (Figs. 13a, b). Pupa: shape similar to that of *P. nora ardates*, abdomen and thorax pale brown, head and wings light greenish brown, marked variably with dark brown blotches (Figs. 13c, d). Similar to those illustrated by Igarashi & Fukuda (1997) from Sumatra (subspecies not identified) except that the Sri Lankan larvae are more greenish and the markings more indistinct. Ants were not observed attending any larvae.

Larval food plants: The current study showed that *Samanea saman* and *Albizia odoratissima* (Fabaceae) are larval food plants in Sri Lanka. The larva feeds only on the flowers.

P. dubiosa indica has a slightly more restricted distribution than *P. nora ardates*—it is common in the dry and intermediate zones but less common in the wet zone and ascends the hills to about 800 m asl. *Samanea saman* is a large introduced tree that is widely planted across the country in all climatic zones (except the arid zone) up to about 600 m asl. *Albizia odoratissima* is commonly planted in the dry and intermediate zones and less commonly in wetter areas



Figure 13. *Prosotas dubiosa indica*. a. Larva, final instar, dorsal view. b. Larva, final instar, lateral view. c. Pupa, heavily marked, dorso-lateral view. d. Pupa, lightly marked, dorso-lateral view.

(Dassanayake, 1980). Since the distribution of the butterfly is much wider than the distribution of these two plants, there must be other plants used, including native species. Igarashi & Fukuda (1997) reported *P. dubiosa* (subspecies not identified) feeding on *Acacia intsia* (Fabaceae) in Sumatra. Robinson *et al.* (2010) report it additionally feeding in other countries on Proteaceae and Sapindaceae but we have not been able to review the references.

Tarucus nara (Kollar, 1848). Striped Pierrot.

Both *T. nara* and *T. callinara* are found in Sri Lanka and India but their status in these two countries was a source of contention in the past. For instance, Moore (1980), de Nicéville (1890), Bell (1915, 1918a) and Ormiston (1924) believed that the species found in India and Sri Lanka was *T. theophrastus* which is now recognized to occur only in Africa, the Middle East and southern Spain. Bethune-Baker (1918) proved by morphology of the genitalia and androconia that *T. nara* and *T. callinara* were two distinct species and were not the same as *T. theophrastus*. Moore (1980) described and illustrated what he termed '*T. theophrastus*.' The illustration however clearly depicts *T. callinara* though the description is too general and could apply to either *T. nara* or *T. callinara*. He did not list *T. nara*. de Nicéville (1890) thought that all individuals found in India and Sri Lanka were *T. theophrastus* and described its egg, larva and pupa. Despite this claim, he listed and described the adults of *T. nara* and *T. callinara* "...for facility of further study", but listed locations in India for both species. In Sri Lanka, Ormiston (1924) listed only *T. theophrastus* but described two forms and said "I have taken both forms together, and they apparently grade into one another, and I regard them as only seasonal varieties." He seems to have been unaware of Bethune-Baker's article. Woodhouse (1949) listed only *T. nara* which he equated with *T. theophrastus*. He quoted from Ormiston (1924), the description of the larva and pupa from de Nicéville (1890), and the larval food plant from Bell (1915). However, the illustration (Plate 19, #1 & 2) is that of *T. callinara*. d'Abrera (1998) contended that there were two species of *Tarucus* in Sri Lanka: *T. nara* was found in the north and northeast and *T. callinara* in the south and southeast. He wrote that the early stages of *T. nara* were "similar to *Castalius rosimon*" and "attended by ants" and that the early stages of *T. callinara* were "not recorded but would undoubtedly confirm specific differences between it and *T. nara*."

According to our new observations, the descriptions of the egg and larva from de Nicéville (1890) and the egg, larva and pupa from Bell (1918a) fit the description of *T. nara* with the following differences:

a) in the larva, S2 with a green dorsal patch with brownish hairs, purple supraspiracular spots on S3–S14, some individuals with reddish-purple subdorsal patch on S11–S13 (Figs. 14a–c); b) in the pupa, variable in color and markings—head and thorax light green to brownish green, abdomen cream to brownish-green with varying amounts of black dorsal, subdorsal and lateral spots, spiracles pale pink (Figs. 14d–g).

Additional notes on immature stages: Early instar: similar to final instar but without the red markings on the dorsal line (Fig. 14h). DNO and TOs visible from the 3rd instar. We observed the larvae being attended by ants (species not identified) on only one occasion (Kayts Island, December 2011) (Fig. 14i).

Larval food plants: There are no reports of larval food plants of *T. nara* in Sri Lanka. The current study showed for the first time that *Ziziphus mauritiana* (Rhamnaceae) is a larval food plant in Sri Lanka. In the early instars, the larva feeds on tender leaves but in the later instars it feeds on maturing leaves and seldom on fully matured leaves.

Note: Bell (1915) (quoted in Woodhouse, 1949) writing of *T. theophrastus* said that "the genus of the foodplant seems to be of little importance as long as the ants are there.... [it has been bred] on Rhamnaceae (*Ziziphus* [sic]), and other plants, such as Mistletoe, Jasmine, &c...." This does not appear to be the case in Sri Lanka.

In Sri Lanka, *T. nara* has been currently recorded only in the northern areas of the arid zone—Jaffna, Kayts Island, Mandativu Island, Mannar, Arippe and Murunkan. *Ziziphus mauritiana* is common in the dry and arid zones (Jaffna, Mannar, Puttalam, Trincomalee, Hambantota, Yala) (Dassanayake, 1996) where it is found near the coast, often on the beach. The distribution of *Z. mauritiana* fits the distribution of *T. nara* in that this plant has been found wherever the butterfly has been recorded and it is likely that *T. nara* feeds exclusively on it. It is interesting to note that despite the fact that *Z. mauritiana* has been planted extensively in home gardens and on roadsides near shops in the lowlands of all climatic zones for shade and its fruits, the butterfly has never been observed in these areas. This suggests that rainfall and temperature may be limiting factors in the distribution of the butterfly.

Note: Ormiston was a careful observer of butterflies and his statement (1924) that he has "taken both forms together and they apparently grade into one another" needs to be taken seriously. However, we have not encountered any intermediate forms in the field nor were any seen in the collections at the NHM (London). We have not been able to study Ormiston's collection at the Bombay Natural History Society though it is reported to be in a poor state.

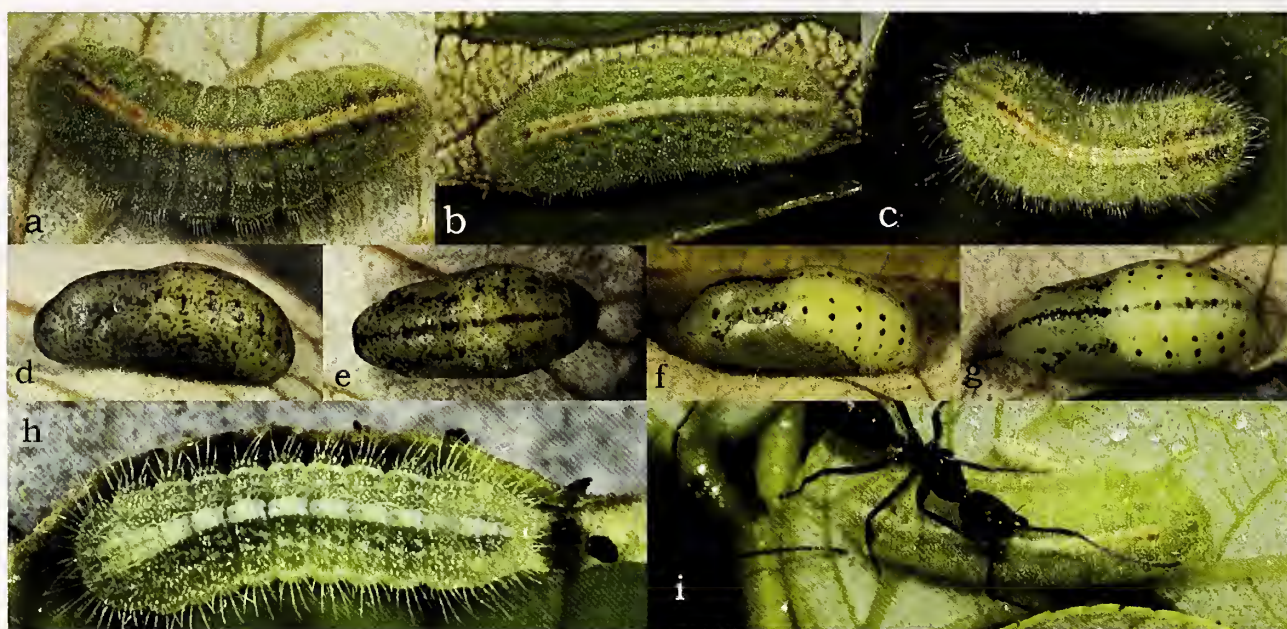


Figure 14. *Tarucus nara*. a. Larva, final instar, dorsal line reddish. b. Larva, final instar, dorsal line white with red. c. Larva, final instar. d. Pupa, darker form, lateral view. e. Pupa, darker form, dorsal view. f. Pupa, lighter form, fewer black markings, dorso-lateral view. g. Pupa, lighter form, dorsal view. h. Larva, early instar. i. Larva, attended by ants.

Tarucus callinara Butler, 1886. Butler's Spotted Pierrot.

See the discussion under *T. nara* regarding the confusion of the genus *Tarucus* in Sri Lanka. In the current study, the final instar larva and pupa are described and the larval food plant identified in Sri Lanka for the first time.

Notes on immature stages: Eggs were laid on the underside of the young leaves of the larval food plant; most were placed a few centimeters off the ground. Larvae and pupae were found on the underside of leaves that were within 12 centimeters of the ground, often overlaid with branches above. The physical barrier thus created and the extremely spiny nature of the larval food plant made it very difficult for birds and lizards to prey upon them. Final instar: body green with a cream-colored dorsal stripe, faint, whitish, short diagonal wavy lines dorso-laterally, dorsal patch on S2 green, entire body covered with numerous setae, those just above the lateral margin much longer; the larva looks less "frosted" than *T. nara* (Fig. 15a). The feeding style of the larva is characteristic—the cells on the underside of the leaf are eaten away in bands leaving the upper epidermis intact; the epidermal cells dry up and break off with time leaving a characteristic pattern on the leaf. No ant/larval associations were observed although a DNO and TOs are present. Pupa: variable in color



Figure 15. *Tarucus callinara*. a. Larva, final instar. b. Pupa, pale straw-yellow with few markings, dorsal view. c. Pupa, same as 10b, lateral view. d. Pupa, pale straw-yellow with no markings. e. Pupa, light greenish, heavily speckled with black.

and markings; color ranged from pale straw yellow to dark dirty green; some individuals heavily speckled with black, others with only three rows of spots on the abdomen, while others were completely devoid of markings (Figs. 15b–e).

Larval food plants: The current study showed that *Ziziphus mauritiana* (Rhamnaceae) is a larval food plant in Sri Lanka. The larva feeds on tender leaves in the early instars. In the later instars it feeds on maturing leaves but seldom on fully matured leaves. Lab-reared larvae refused a closely allied species, *Ziziphus oenoplia*.

In Sri Lanka, *T. callinara* has been currently recorded only in the southern areas, usually near the coast—Tissamaharama, Hambantota, Kirinde and Yala. *Ziziphus mauritiana* is common in the dry and arid zones (Jaffna, Mannar, Puttalam, Trincomalee, Hambantota, Yala) (Dassanayake, 1996) where it is found near the coast, often on the beach. The distribution of *Z. mauritiana* fits the distribution of *T. callinara* in that this plant has been found wherever the butterfly has been recorded and it is likely that *T. callinara* feeds exclusively on it. It is interesting to note that although its food plant is found in the northern areas, the butterfly is not. Though *T. nara* and *T. callinara* use the same food plant and have similar behaviors and habitat requirements, their distributions appear not to overlap in Sri Lanka. Other species of the genus *Tarucus* have been reported as feeding on *Ziziphus* in India (K. Kunte, pers. comm.) and South Africa (Woodhall, 2005).

Subfamily: Theclinae
Tribe: Arhopalini

Arhopala centaurus pirama (Moore, 1881). Centaur Oakblue.

The final instar larva and pupa of *A. centaurus pirama* (as *Nilasera pirama*) were described briefly by Moore (1880) from Sri Lankan material. In India, the larva and pupa of *A. centaurus* were described briefly by Davidson & Aitken (1890) and in detail by Bell (1919). The findings of the current study agree with the brief descriptions of the larva given by Moore and Davidson & Aitken except that these descriptions do not describe the larva fully. Davidson and Aitken (1890) stated that they saw no erectile organs on S12 but they are present (Fig. 16a) in Sri Lankan individuals. The detailed description by Bell (1919), however, does not quite fit the Sri Lankan specimens. In Sri Lanka, the final instar larva has ground color light green to white and all specimens studied had the following



Figure 16. *Arhopala centaurus pirama*. a. Eversible organs. b. Larva, final instar, dorso-lateral view, with ants. c. Larva, final instar, dorsal view. d. Pupa, lateral view. e. Closeup of lateral markings that appear like ant's heads with eyes.

markings: S3–S4 with a reddish brown lateral marking along the anterior edge; S5–S11 with a reddish-brown oval lateral marking, each with a black spiracle in the center surrounded by a few black setae (posterior to these markings is variably dark to light blackish); S2 with subdorsal and lateral reddish brown stripes that meet posteriorly; S12–S14 indistinctly separated, with a narrow reddish-brown dorsal band, broadest on S14; DNO on S11. Variable characteristics include: S5–S11 with two white wavy lines (the lower one somewhat indistinct) separated by a black or dark reddish-brown band; the dorsum usually brick red but sometimes with diffuse yellow and black markings (Figs. 16b–c). In the current study, the pupa is reddish-brown, wings white with a tint of brown, and head light reddish-brown (Fig. 16d). We have not seen a green pupa (as per Moore,

1881) or a dark brown pupa (as per Bell, 1919).

Additional notes on immature stages: In the field, the 3rd–5th instars and pupa were always attended by ants (*Oecophylla smaragdina*) (this obligatory and species-specific association has been known for a long time, e.g. Davidson & Aitken, 1890) which fiercely guarded their charge but they did well in the lab without them. Observations have not been made for the 1st and 2nd instar. The fifth instar is quite extraordinarily marked. From above, the black spiracle within the reddish-brown spot resembles the head and eyes of a red ant remarkably well—the larva looks like a congregation of red ants and not a larva, thus potentially protecting it from avian or wasp predators (Fig. 16e) but not from parasitoids: many larvae collected in the field were parasitized by two or three different species of braconid wasp (species not identified).

Larval food plants: In Sri Lanka, Moore (1880), quoting from Thwaites, reported *Schleichera trijuga* [now *S. oleosa*]. Woodhouse recorded “Combretaceae, Lythraceae” (but with no reference) and *Terminalia paniculata* (quoting from Davidson *et al.*, 1896, from India). The current study showed that *Syzygium cumini* (Myrtaceae) (H. D. Jayasinghe, pers. comm.), *Lepisanthes tetraphylla* (Sapindaceae) and *Elaeocarpus serratus* (Elaeocarpaceae) are used as larval food plants in Sri Lanka. The larva feeds on tender leaves. *Terminalia paniculata* does not occur in Sri Lanka though other species of *Terminalia* are found here. We have not been able to confirm whether or not *S. oleosa* is used though it is a common plant. *A. centaurus* is highly polyphagous. For example, Igarashi & Fukuda (2000) reported host plants in the families Fagaceae, Combretaceae, Tiliaceae and Lythraceae from various regions in SE Asia. Vane-Wright & Gaonkar (2006) clarified the widespread misuse of the names *A. centaurus* and *A. pseudocentaurus*.

A. centaurus pirama is uncommon and seasonal. It is found in the lower elevations of the wet zone but is more common in the dry and intermediate zones. *Lepisanthes tetraphylla* is common in the forests of the dry and intermediate zones and rare in the wet zone (Dassanayake, 1998). *Elaeocarpus serratus* is common in the forests of the wet and the moist intermediate zones (Dassanayake, 1995). The distribution of the host ant in Sri Lanka has not been systematically studied though it is most common in the dry and intermediate zones, and scarce in the arid and wet zones. Since the larva-ant relationship is obligate, the presence of the ant is a limiting factor as long as an acceptable larval food plant is found. The distributions of these larval food plants match that of the butterfly in that at least one of these plants has been found wherever the butterfly has been recorded though given the high degree of polyphagy recorded for the butterfly, there may be additional larval food plants used, possibly other species of *Lepisanthes* and *Elaeocarpus*.

Arhopala amantes amantes (Hewitson, 1862). Large Oakblue.

The final instar larva and pupa of *A. a. amantes* were described briefly by Moore (1880) presumably from Sri Lankan material. In India, the larva and pupa of *A. amantes* were described briefly by Davidson *et al.* (1897) and in detail by Bell (1919). The findings of the current study agree with these descriptions except for the following: a) the ground color of the final instar larva is pale yellowish-green or reddish-brown and S7–S9 often with an indistinct subdorsal black patch (Figs. 17a–c); and b) the color of the pupa is variable: some have a pale light green thorax, white wings and pale reddish-brown abdomen (darker towards the tip) with spiracles on S9–S11 surrounded by long setae; others have a greenish-grey thorax, wings light brown with dark brown striations between the veins, and abdomen dark reddish-brown with black blotches (Figs. 17d–g). It normally pupates within a leaf.

Additional notes on immature stages: Egg: dome-shaped, flattened at base, honeycombed with fine projections (Fig. 17h). 1st instar: newly hatched—head yellowish-orange, body pale brownish-yellow with a darker lateral band, S10–S11 with a light purplish dorsal blotch, typical lycaenid shape with long setae on the dorso-ventral margin (Fig. 17i). 2nd: pale yellowish-green but shaped as per final instar larva, S3–S10 darker green dorsally, S14 depressed dorsally, setae long and pinkish (Figs. 17j, k). From 2nd to 5th instar, the larva changes color and pattern as it ages within the instar. 3rd: ground color varies depending on the color of the young leaves on which it rested and fed (some trees have pale yellow young leaves; others reddish); body light reddish-brown or yellowish-green, wide brownish-green dorsal band on S3–S10 bordered by a thin greenish-yellow line which extends to S2 and S14, S2 yellow anteriorly, S14 yellow posteriorly, spiracles off-white (Figs. 17l, m). 4th: similar to 3rd (with two color forms) but colors more saturated, dorsal band brownish-green at the center and yellowish-green with diffuse red areas at the edges, yellow line darker, and a light reddish line below this, S2 with a dome-shaped yellow dorsal area (Figs. 17n, o). In the field, the 3rd–5th instar larvae were attended assiduously by red ants (*Oecophylla smaragdina*) which fed from the DNO (Fig. 17p) but they developed normally in the lab without them. Larvae were parasitized by a wasp (Braconidae: species not identified) whose larvae emerged in the fifth instar (Figs. 17q, r). In one instance, a first instar larva that was collected and reared in the lab was parasitized though the parasitic larvae did not appear until the 5th instar. It is possible that the butterfly larva was parasitized during the 1st instar and that the eggs or larvae of the parasite remained dormant until the caterpillar's 5th instar (Seufert & Fiedler, 1999). Duration of immature stages (days): pupa (11); egg to emergence of adult (43).

Larval food plants: Woodhouse (1949) listed “Leguminosae, etc., and where there are red ants’ nests. *Hopea*, *H. jucunda*, *Lagerstroemia*, *L. flos-reginae* [now *L. speciosa*], *Terminalia catappa*, etc.” but with no source. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Syzygium cumini* (Myrtaceae) and *Terminalia chebula* (Combretaceae). The larva feeds only on tender

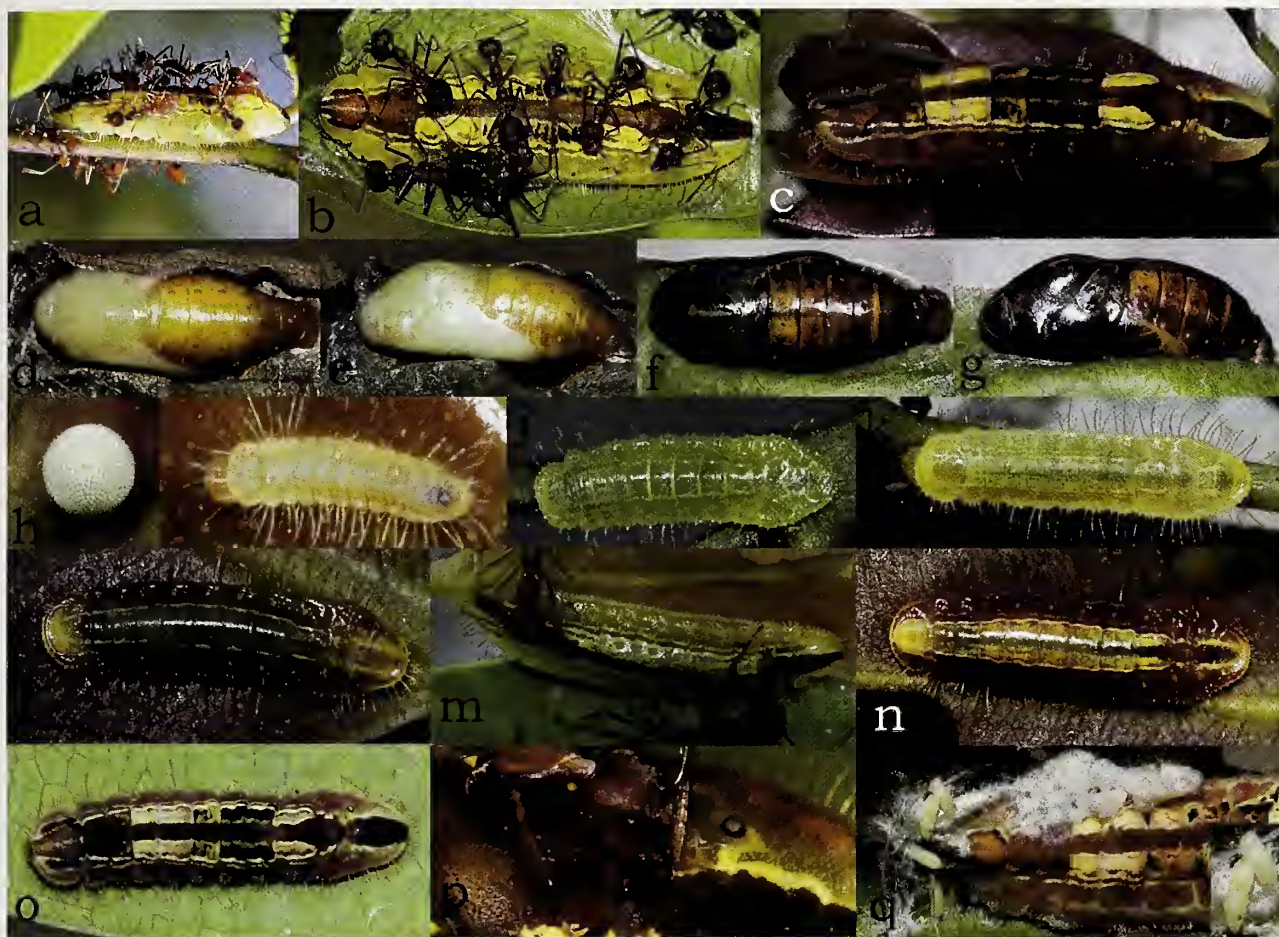


Figure 17: *Arhopala amantes amantes*. a. Larva, fifth instar, pale yellowish-green ground color, with ants, lateral view. b. Larva, fifth instar, pale yellowish-green ground color, with ants, dorsal view. c. Larva, fifth instar, reddish-brown ground color, dorso-lateral view. d: Pupa, light colored form, dorsal view. e: Pupa, light colored form, lateral view. f. Pupa, dark colored form, dorsal view. g. Pupa, dark colored form, lateral view. h. Egg. i. Larva, first instar, head visible, dorsal view. j. Larva, early second instar, dorsal view. k. Larva, later second instar, head visible, dorsal view. l. Larva, early third instar, dorsal view. m. Larva, late third instar, with ants, dorsolateral view. n. Larva, early fourth instar, dorsal view. o. Larva, late fourth instar, dorsal view. p. *Oecophylla smaragdina* feeding from DNO on S11. q. Parasitized larva with braconid wasp larvae emerging and spinning pupal cocoons. r. Close up of braconid wasp larvae.

leaves. We have not been able to confirm the use of *H. jucunda*, *L. speciosa* or *T. catappa* though these plants are found in Sri Lanka.

A. a. amantes is widespread below 300 m asl in all climatic zones. *Syzygium cumini* is widespread in the dry and intermediate zone forests, particularly along streams and tanks (man-made lakes) (Dassanayake, 1981a). *Terminalia chebula* is widespread in the dry and intermediate zones in open savannah and grasslands (Dassanayake, 1995). The larval food plant that is used by the butterfly in the wet zone is not known but is likely to be a species of *Syzygium* or *Terminalia* which have representatives there. *A. amantes* is an obligate myrmecophile and has been reported to be highly polyphagous (a trait usually associated with this

condition). For example, Robinson *et al.* (2010) listed Combretaceae, Dipterocarpaceae, Lythraceae, and Leguminosae in other countries, though we have not been able to review these references. The distribution of the host ant will also limit the distribution of the butterfly.

Arhopala ormistoni Riley, 1920. Ormiston's Oakblue. Endemic.

In the current study, the immature stages are described and the larval food plant identified for the first time.

Notes on immature stages: Although oviposition by the ♀ has not been observed in the field, a single 3rd instar larva that was collected on a very young

leaf of the larval food plant at a height of about 2 meters produced an adult male of *A. ormistoni* at emergence. A few ants (species not identified) were found on the larva when it was collected, but it appears to have no obligatory relationship for completing its life cycle successfully. The larva ate voraciously and developed very quickly, presumably to avoid the prospect of having to eat the rapidly maturing leaves that turn tough and unpalatable, and possibly toxic. The larva reared in the lab wandered around before pupation and settled on a dried leaf to pupate. 3rd instar: head pale pinkish-yellow, ground color pale yellowish-brown with red, white and green markings, S2–S10 with red and green interrupted dorsal line, subtended by a white interrupted band, then by a greenish band, then by a white interrupted band, spiracles white with a reddish transverse diffuse band above and below, S2 shield-like with a central dome, DNO on S11 and eversible tentacles on S12, entire body covered with small reddish setae giving a frosted appearance, similar but longer setae on dorso-ventral margin (Fig. 18a). 4th: ground color darker reddish-brown, S2–S14 with continuous green dorsal line, subtended by broad cream-colored band which has light reddish to brownish patches at its borders, spiracles white and surrounded by red markings, S2 with a pair of small red spots anteriorly, center of dome with green triangular mark, edges translucent white, lateral margins as in ground color (Fig. 18b). 5th: ground color pale purplish-green, more or less translucent, S2–S14 dorsal line dark purplish, diffuse pinkish markings on either side from S4–S10, spiracles surrounded by diffuse reddish patches (Fig. 18c). All instars studied were superbly camouflaged amidst the leaves of its larval food plant. Pupa: similar in shape to that of *A. centaurus piriama*, ground color pale brownish-green with light brown and black markings, more extensive on the head and thorax, spiracles white surrounded by beige, series of subdorsal black spots on the abdomen (Figs. 18d, e). Duration of immature stages (days): 4th instar (3); 5th (3); pupa (10).

Larval food plants: The current study showed for the first time that *Vateria copallifera* (Dipterocarpaceae) is a larval food plant in Sri Lanka. The larva feeds only on tender leaves. The use of members of the family Dipterocarpaceae is rare among butterflies but does show up in the Arhopalini (Megens *et al.*, 2005).

A. ormistoni is restricted to lowland dipterocarp forests in the wet zone (Kanneliya, Morapitiya, Sinharaja, Meetirigala) with a disjunct population in a wet zone-like forest at Nilgala in the dry zone. *Vateria copallifera* is widespread and common in the wet zone below 1000 m asl (Dassanayake, 1980) though it has not been recorded from Nilgala. At

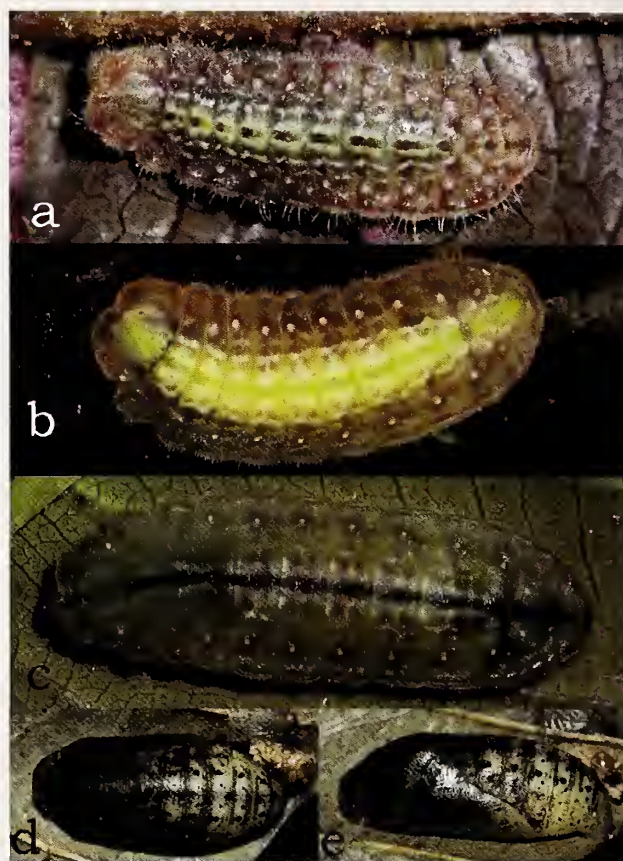


Figure 18. *Arhopala ormistoni*. a. Larva, third instar. b. Larva, fourth instar. c. Larva, fifth instar. d. Pupa, dorsal view. e. Pupa, dorso-lateral view.

Nilgala the butterfly was seen near *Vatica obscura* (Dipterocarpaceae), which is perhaps the larval food plant used in that area.

Arhopala abseus mackwoodi (Riley, 1923). Aberrant Bushblue. Endemic subspecies.

The immature stages and larval food plant of *A. abseus mackwoodi* in Sri Lanka have not been described, nor have the immature stages of *A. abseus* in India been described by the usual authors (Bell 1919; Davidson & Aitken 1890; Davidson *et al.*, 1896). Igarashi & Fukuda (1997) illustrated the final instar larva and pupa of *A. abseus* in Thailand (no subspecies identified) but could not identify the larval food plant. In the course of the current study, we have not yet encountered eggs, larvae or pupae though adults have been seen on many occasions at a few locations. However, a larva was found and raised on the tender leaves of *Vateria copallifera* (Dipterocarpaceae), but no description of the larva or pupa is available (H. D. Jayasinghe, pers. comm.).

Surendra quercetorum discalis Moore, 1857. Common Acacia Blue.

The immature stages of *S. quercetorum discalis* in Sri Lanka have not been described. In India, the final instar larva and pupa of *S. quercetorum* were described by Davidson *et al.* (1896) and Bell (1919). Woodhouse (1949) quoted from Bell (1919). The current study agrees with these descriptions with the following exceptions: a) the final instar is more variable than described by Bell (1919) and it has two forms: a green form (similar to that described by Bell 1919 except that some larvae are completely green without any pink and the dorsal band is sometimes absent) (Fig. 19a) and a dark purplish-brown form (Fig. 19b). The markings on the purplish-brown form are similar to those on the green form but the lateral diagonal lines are dark pinkish-brown; b) the pupa has a girdle (Davidson *et al.* reported it was fastened only by the tail though Bell reported the girdle) and the extent of black blotching is variable with some specimens having sparse markings (Figs. 19c, d). A DNO and TOs are visible in the 5th instar.

Additional notes on immature stages: The ♀ sometimes laid 6–10 eggs in a closely spaced group though it usually laid one or two. Some eggs have a pink tinge (Fig. 19e). The egg and larva are almost always attended by ants (species not identified) but the relationship is not obligate as larvae developed normally in the lab without ants. We have not observed eggs or larvae on plants that are without the ants. The ♀ often walked along the branches before oviposition, presumably to verify the presence of ants. Sometimes, ants rushed towards her and either touched or climbed onto the abdomen, perhaps to signal that they were present (Fig. 19f). The final instar larva often forms a shelter by loosely joining several leaves together (Fig. 19g). One specimen of an early instar was entirely green with only faint dorsal markings (Fig. 19h). One larva was found that was parasitized by a dipteran (Fig. 19i). Once the dipteran eclosed, the parasitized larva was then attacked by the ants that previously attended it (Fig. 19j). It appears that the ants benefit whether or not the larva is parasitized, either as a source of sugar or a source of protein. It is unclear what benefit the larva gains from this relationship especially when the ♀ seeks out the ants to lay its eggs. Duration of immature stages (days): pupa (11).

Larval food plants: In Sri Lanka, Woodhouse listed *Acacia caesia* and *A. pennata* after Bell 1915 [sic] (the actual reference is Bell 1919). The current study showed for the first time that *Calliandra surinamensis* (Fabaceae) is a larval food plant in Sri Lanka and confirmed the use of *A. caesia* and *A. pennata* (Fabaceae) as larval food plants in Sri Lanka. The larva feeds only on tender leaves and on the exudates from the extrafloral nectar gland at the base of the leaf (Fig. 19h). The same behavior was noted for the related *S. florimel* from Malaysia (Fiedler, 1992b). Igarashi & Fukuda (2000) reported *S. quercetorum* feeding on *A. catechu* in India, and Veenakumari *et al.* (1997) reported *S. quercetorum* [sic] *latimargo* feeding on a species of *Acacia* in the Andamans and Nicobar Islands.

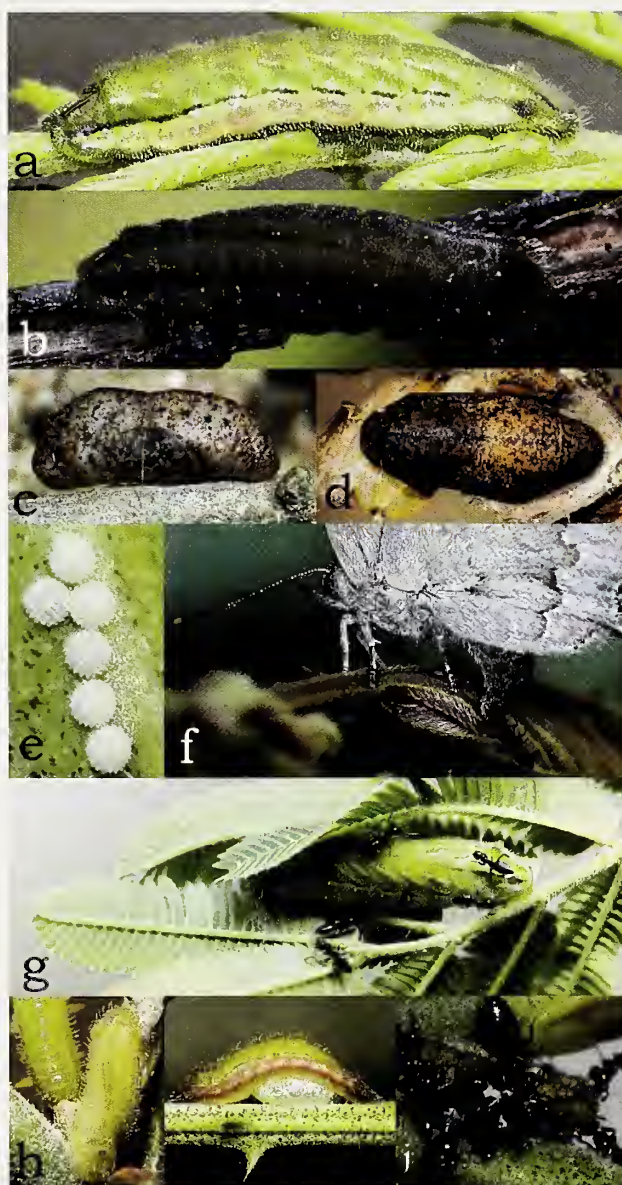


Figure 19. *Surendra quercetorum discalis*. a. Larva, fifth instar, green form. b. Larva, fifth instar, purplish-brown form. c. Pupa, lateral view. d. Pupa, dorsal view. e. Eggs. f. Female attended by ant while ovipositing. g. Larva, fifth instar, attended by ants within its leaf shelter. h. Larva, early instar (entirely green) feeding on gland at the base of the leaf. i. Parasitized larva with dipteran pupa case beneath. j. Parasitized larva being eaten by its former attendant ants

S. quercetorum discalis is found all over the island in the dry, intermediate and wet zones up to about 800 m asl. *Calliandra surinamensis* is an introduced ornamental that is widely planted in the intermediate and wet zones. *Acacia caesia* is a native that is found in all climatic zones up to about 500 m asl. *A. pennata*

is a native that is found in the dry and intermediate zones only. The distribution of these plants matches that of the butterfly in that at least one of these plants has been recorded wherever the butterfly is found.

Subfamily: Theclinae

Tribe: Hypolycaenini

Hypolycaena nilgirica Moore, [1884]. Nilgiri Tit.

In the current study, the immature stages are described and the larval food plants, which are members of the Orchidaceae, are identified for the first time.

Notes on immature stages: Eggs were laid singly, in large numbers, anywhere on the orchid including the inflorescence and stem for ground orchids, and the aerial roots and flowers for epiphytic orchids (Fig. 20a). Many eggs collected in the field were parasitized by an unidentified parasitoid. 1st instar: newly emerged larva: fed on the buds and flowers of the inflorescence, the stem or aerial roots depending on the species of orchid; head pale brown, body translucent greenish-yellow (sometimes almost white), faint greenish dorsal line, and pink subdorsal line, and between these two lines, two long black setae on each segment, similar set of setae dorso-ventrally, S2 with a hemispherical translucent dorsal depression (Fig. 20b). 2nd: ground color ranges from pale pink to pale green to almost white, otherwise similar to 1st instar except that dorsal line and subdorsal band are red, often with a light pink lateral line; DNO visible (Fig. 20c). 3rd: head brown, body with numerous small setae giving it a frosted appearance, purplish dorsal band, more prominent in anterior segments, faint purplish subdorsal discontinuous line, spiracles black surrounded by purple, dorso-ventral fold commonly edged with a purple band; TOs visible (Fig. 20d). 4th: similar to 3rd (Fig. 20e). 5th: Most larvae with a purplish dorsal line, a thinner, less well-defined white dorso-lateral line, adjacent to this a pinkish line, and a well-defined purplish-pink dorso-ventral margin below the spiracles, but some individuals are devoid of any banding, spiracles distinct and dark brown, body covered with numerous setae giving it a fuzzy frosted appearance, S12 with eversible tentacles (rarely displayed), S11 with DNO (Figs. 20f–h). Some larvae were attended by ants (species not identified) but most were not despite the presence of the DNO. Larvae reared in the lab without any ants developed into normal adults. Coloration of larva seems to match that of its substrate, offering a remarkable degree of crypsis on the variably colored parts of the plant.

Pupation commonly occurred on the plant (on the inflorescence or immediately below it



Figure 20. *Hypolycaena nilgirica*. a. Egg. b. Larva, first instar. c. Larva, second instar, intermediate color form. d. Larva, third instar, green form. e. Larva, fourth instar, pink form. f. Larva, fifth instar, green form. g. Larva, fifth instar, mixed color form. h. Larva, fifth instar, white color form (on white flower). i. Pupa, lateral view, on stem of ground orchid. j. Pupa, dorsal view, as per (i). k. Pupa, lateral view, on aerial root of epiphytic orchid. l. Pupa, dorsal view, as per (k).

for ground orchids; elsewhere on the plant for epiphytes), with head pointing down and attached to substrate by a very wide cremaster and a girdle. Pupa: well camouflaged, colored less variably than larva, smooth, ground color green with diffuse purplish area on dorsum of thorax, two distinct dark areas just above the wing, spiracles white except that on S2 black, surface often covered with minute white markings (Figs. 20i, j). Some pupae have whitish or pinkish markings along the lower margin of the wing buds (Figs. 20k, l). Duration of immature stages (days): 1st instar (2); 2nd (3–4);

3rd (3); 4th (4–6); 5th (4–6); pupa (9–11); egg to emergence of adult (25–27).

Larval food plant: The current study showed for the first time that various species of Orchidaceae are used as larval food plants in Sri Lanka including *Malaxis versicolor* (flowers) (H. D. Jayasinghe, pers. comm.), *Peristylus trimenii* (flowers) (H. D. Jayasinghe, pers. comm.), *Vanda* sp. (cultivated) (aerial roots) (P. D. Dissanayake, pers. comm.), *Arundina graminifolia* (flowers and flower buds), *Spathoglottis plicata* (flowers and flower buds), *Arachnis flos-aeris* (aerial roots), *Vanda tessellata* (aerial roots, flowers, flower buds) and *Vanda testacea* (aerial roots). Those feeding on aerial roots prefer the actively growing tips but in the lab fed on the inside of older roots as well. Various species of *Hypolycaena* (in the subgenus *Chliaria*) are also reported to be specialists on the Orchidaceae, e.g. *H. othona* in Malaysia (Fiedler, 1992a) or *H. danis* in Australia (Braby, 2000), though other species like *H. erylus* feed on a wide range of plants (e.g. Veenakumari *et al.*, 1997 in the Andamans and Nicobar Islands).

H. nilgirica was reported as being rare though widespread (Woodhouse, 1949) but current records show it to be more common, at least during its flight season, and more widely distributed. It is found in the dry, intermediate and wet zones up to about 800 m asl. *M. versicolor* is a native ground orchid that is fairly common in shady places in submontane, midcountry, and subtropical montane forests. *H. nilgirica* was observed using this plant in Nilgala which is technically in the dry zone but some of its forest has the character of a wet zone forest. *P. trimenii* is a rare endemic orchid that grows in shade near streams in the eastern intermediate zone. *A. graminifolia* is an introduced ground orchid that has now become naturalized and is well-established in the wild. It occurs near seepages at the bottom of hills and in moist meadows of the wet lowlands and hills. *S. plicata* is an introduced ground orchid, which is more widely grown in home gardens and is much less invasive than *A. graminifolia*; it is found in the wet zone lowlands up to 500 m asl where it is naturalized in some places. *Arachnis flos-aeris* is an introduced epiphyte that is widely cultivated in home gardens in the dry, intermediate and wet zones. *Vanda tessellata* is a native epiphyte that is common on trees in dry and intermediate zone forests and along the east coast. *Vanda testacea* is a native epiphyte that is common on trees along roadsides and in the wet lowlands and the forests of the dry and intermediate zones up to the mid-elevations (Dassanayake, 1981a; Fernando & Ormerod, 2008). *H. nilgirica* successfully exploits exotic orchids, which tend to be more prolific and less seasonal in their flowering behavior, and this has allowed a once rare butterfly to become

much commoner. Braby (2000) reported a similar phenomenon in Australia where *H. danis* has become a pest of garden orchids. It is likely that other native and cultivated orchids are also used as larval host plants.

Subfamily: Theclinae

Tribe: Iolaini

Pratapa deva deva (Moore, [1857]). White Royal.

The immature stages of *P. d. deva* in Sri Lanka have not been described. In India, the final instar larva and pupa of *P. deva* were described by Davidson *et al.* (1896) and Bell (1919). In the current study, the final instar and pupa were reared by H. D. Jayasinghe. The descriptions of Davidson *et al.* (1896) and Bell (1919) agree with his results except for the following: a) in the larva, the spiracles are white, ringed with brown (Figs. 21a, b), and b) in the pupa, the wing buds are light purplish-brown and their bases are white (Figs. 21c, d). Bell (1919) reports the presence of a DNO and faint TOs. No ants were observed attending the larva or pupa. The pupa illustrated by Igarashi & Fukuda (1997) from Malaya (no subspecies given) is much whiter overall, agreeing with the description of the Indian specimens.

Larval food plant: In Sri Lanka, Woodhouse listed “*Loranthus tomentosus* [now *Taxillus tomentosus*] and *L. scurrula* [now *Scurrula parasitica*]” after Davidson *et al.* (1896). The current study showed for the first time that *Scurrula cordifolia* is a larval food plant in Sri Lanka (S. Sanjeeva, pers. comm.) and confirmed the use of *Taxillus tomentosus* (Loranthaceae) (H. D. Jayasinghe, pers. comm.). The restriction to members of the family Loranthaceae has been recorded in the whole region (e.g. Igarashi & Fukuda, 1997; Veenakumari *et al.*, 1997).

P. d. deva has been reported only from the Uva province in the southeast of the island. *Scurrula cordifolia* is found scattered in the dry and intermediate zones while *Taxillus tomentosus* is common in the Uva basin and scattered in the intermediate zone (Dassanayake, 1987). The distribution of these two species matches the distribution of the butterfly in that at least one of these plants has been found where the butterfly has been recorded and it is unlikely that there is another larval food plant.

Tajuria jehana ceylanica Riley, 1921. Plains Blue Royal. Endemic subspecies.

The immature stages and larval food plant of *T. jehana ceylanica* have not been described, nor have those of *T. j. jehana* in India. In the current study, the immature stages are described and the larval food plant identified for the first time.

Notes on immature stages: Egg: white, dome-shape with honeycombed ridges, laid anywhere on the larval food plant (Fig. 22a). 1st instar: newly emerged larva with head black, body pale yellow, S2 with depressed black dorsal patch and 2 pairs of large black setae that point forward, S3–S10 dark reddish-brown dorsal band, often discontinuous and with black setae and orangish-yellow discontinuous band laterally and subdorsally, S11–S12 light gray dorsally (Fig. 22b); 2nd: shaped as per the final instar (described in detail for *T. cippus* by Bell, 1919), white with blotches brick-red to brown markings, middorsal setae with white tip and base and black at the center and pointing posteriorly, S2 depressed area dorsally black with setae pointing anteriorly, dorso-ventral setae translucent white to pale yellow (Fig. 22c). 3rd: setae are completely lost, head black, body brown and white, S2 with black dorsal triangular patch with 3 lighter colored streaks, S14 with more or less rectangular black dorsal patch, S3–S4 & S11 with large white triangular patch bordered by dark reddish brown, S5–S7 with circular dorsal reddish-brown patch, lighter at center, S8–S9 with white circular dorsal patch mottled with light brown and edged with dark brown, spiracles light blue ringed with black (Figs. 22d–f). 4th: similar to 3rd but larva much broader and flatter and more heavily marked, spiracles light brown (Fig. 22g). 5th: similar to the 4th but dark brown with distinct white patch on S6–S7 extending from dorso-ventral line to subdorsal, spiracles white ringed with black; we have not been able to determine if TOs and a DNO are present (Figs. 22h, i). Pupa: light brown to dark brown to almost black depending on the substrate, heavily blotched with dark colored markings, spiracles white, thorax and abdomen with small dorsal raised projections, shape similar to that of *T. cippus* as described by Bell (1919) (Figs. 22j–l). Pupates on twigs and branches near the base of the larval food plant where it is well-camouflaged (Fig. 22m). Duration of immature stages (days): egg (3–5); 1st instar: (1–2); 2nd (3–6); egg to adult (28–30).

Larval food plant: The current study showed that *Dendrophthoe falcata* (Loranthaceae) is used as a larval food plant in Sri Lanka. The early instar larva feeds only on tender leaves but later instars feed on more mature leaves. Ants have not been observed attending the larvae in the field.

T. jehana ceylanica is found only in the Jaffna peninsula where it is not uncommon. *D. falcata* is widespread in all climatic zones but is particularly common in the dry zone (Dassanayake, 1987). The distribution of the butterfly must be restricted by some factor other than the availability of its larval food plant.

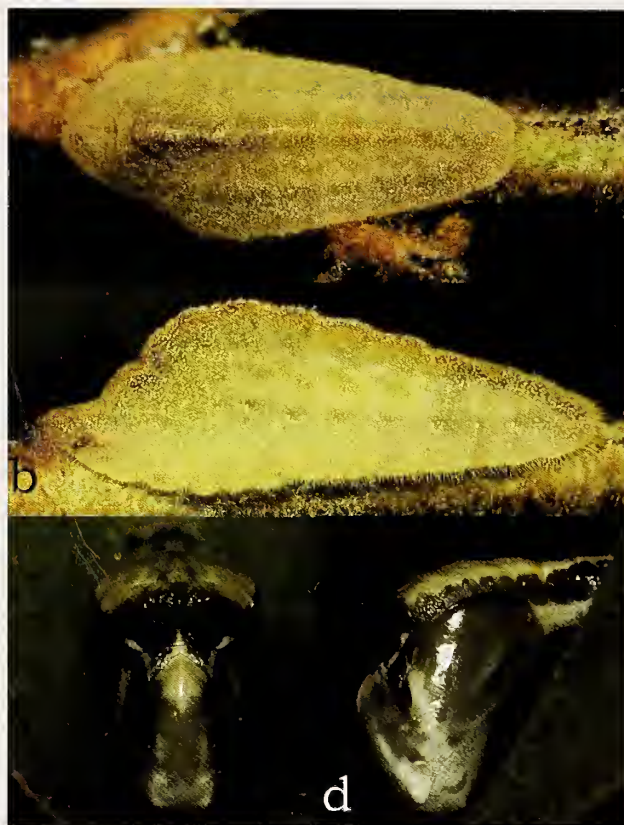


Figure 21. *Pratapa deva deva*. a. Larva, final instar, dorsal view. b. Larva, final instar, lateral view. c. Pupa, dorsal view. d. Pupa, lateral view

Tajuria cippus longinus (Fabricius, 1798). Peacock Royal. Endemic subspecies.

The final instar larva and pupa of *T. cippus longinus* in Sri Lanka were described briefly by Moore (1880). In India, the larva and pupa of *T. cippus* (as *T. longinus*) were described by Davidson *et al.* (1896) and Bell (1919). The findings of the current study agree with the descriptions of Moore and Bell (but not that of Davidson *et al.*) except for the following points: a) the larvae in Sri Lanka were exceptionally variable—the ground color ranged from off-white to brown, reddish-brown, and dark chocolate brown, and the markings were variable in placement and color (Figs. 23a–f); b) the pupa fits the description by Bell but is more variable in color, ranging from light grayish-green to brown and reddish-brown (Figs. 23g–j).

Additional notes on immature stages: Egg: dome-shaped and smooth with a slight depression at the top (Fig. 23k). 1st instar: head straw-colored with two black eyespots and red mouthparts, body pale green with an obscure pale yellow dorsal band, S2 depressed dorsally and with brown hexagonal patch. 2nd: not recorded. 3rd: similar to 1st but body darker green (Fig. 23l). 4th: highly variable in color and markings, ground color varies from light green to reddish-brown to dark brown; most individuals with

a dark colored lateral triangular patch from S7–S10 with the broadest side bordering the ventral margin (Figs. 23m–p). Bell (1919) reports the presence of a DNO and TOs but we did not see them. We have never seen the larva with ants though it is common and often seen. Bell (1919) reports that ants hardly ever attend the larva but occasionally ‘visit’ it. Duration of immature stages (days): pupa (9). One color form is similar to the larva and pupa illustrated by Igarashi & Fukuda (1997) from Hong Kong (subspecies not identified).

Larval food plant: In Sri Lanka, Moore (1880) quoting from Thwaites recorded that it fed on Loranthaceae and Ormiston (1924) recorded that it fed on *Loranthus* [all mistletoe species formerly attributed to the genus *Loranthus* in Sri Lanka have now been transferred to other genera]. The current study showed for the first time that *Dendrophthoe falcata* and *Taxillus cuneatus* (Loranthaceae) are used as larval food plants in Sri Lanka. The first three instars feed on tender leaves while the final two instars feed on more mature leaves. Igarashi & Fukuda (1997) also reported it feeding on Loranthaceae in the Malay Peninsula (subspecies not identified) and Veenakumari *et al.* (1997) reported *T. c. cippus* feeding on Loranthaceae in the Andaman and Nicobar Islands.

T. cippus longinus is widespread below 1000 m asl but is more common in the arid, dry and intermediate zones. *Dendrophthoe falcata* is widespread, but is most common in the dry zone. *Taxillus cuneatus* is more common in the northern areas of the dry and intermediate zone though populations are found in the wet zone near Ratnapura (Dassanayake, 1987). The distribution of these two plants matches the distribution of the butterfly in that at least one of these plants has been found where the butterfly has been recorded but it is possible that other members of the Loranthaceae are also used.

CONCLUSIONS

The immature stages of most of the species documented in this study exhibited some variation in size, color and patterning, particularly in the final instar and pupa. They were, however, similar to those described from peninsular India with which Sri Lanka is zoogeographically related, and to those described from other countries in the Indo-Australian region.

The larval food plants used by the Lycaenids dealt with in this paper are mostly similar or the same at least at the family level as those reported elsewhere. Many species reported here are polyphagous, feeding on plants from different families. Several species are monophagous: *Jamides*



Figure 22. *Tajuria jehana ceylanica*. a. Eggs. b. Larva, first instar, dorsal view. c. Larva, second instar, lateral view. d. Larva, third instar, well camouflaged. e. Larva, third instar, dorsal view. f. Larva, third instar, lateral view. g. Larva, fourth instar, dorso-lateral view. h. Larva, fifth instar, lateral view. i. Larva, fifth instar, dorsal view. j. Pupa, dorsal view. k. Pupa, dorso-lateral view. l. Pupa, dark form, dorsal view. m. Pupa, dark form, well camouflaged, dorso-lateral view.

coruscans and *J. lacteata* (both endemic), *Nacaduba hermus sidoma* and *N. sinhala* (endemic), *Tarucus nara* and *T. callinara*, *Arhopala ormistoni* (endemic) and *A. abseus mackwoodi* (endemic).

Most species were attended by ants only casually: female butterflies oviposited in the field without the presence of ants, and ants were not required for the development of the larva when reared in captivity. Twenty-two species were confirmed to have a DNO and TOs which are ant-associated structures. Only two species are obligate myrmecophiles (*Arhopala centaurus pirama* and *A. a. amantes*), both associating only with *Oecophylla smaragdina*.

Of the species or subspecies dealt with in this paper, 2 are considered Critically endangered (CR) according to IUCN criteria (*Tajuria jehana ceylonica* and *Arhopala ormistoni*); 3 Endangered (EN) (*Pratapa d. deva*, *Arhopala abseus mackwoodi*, *Tarucus callinara*) and 3 Vulnerable (VU) (*Nacaduba sinhala*, *Jamides coruscans* and *J. lacteata*) (van der Poorten, 2012). The information presented in this paper provides some of the base information about the biology of immature stages that is required for conservation work. As well as detailing the larval food plants and ant associations, it also illustrates that the larvae can be successfully raised in the lab should ex-situ conservation measures be needed. More work is required to get a more detailed understanding of the biology of these species in the field.

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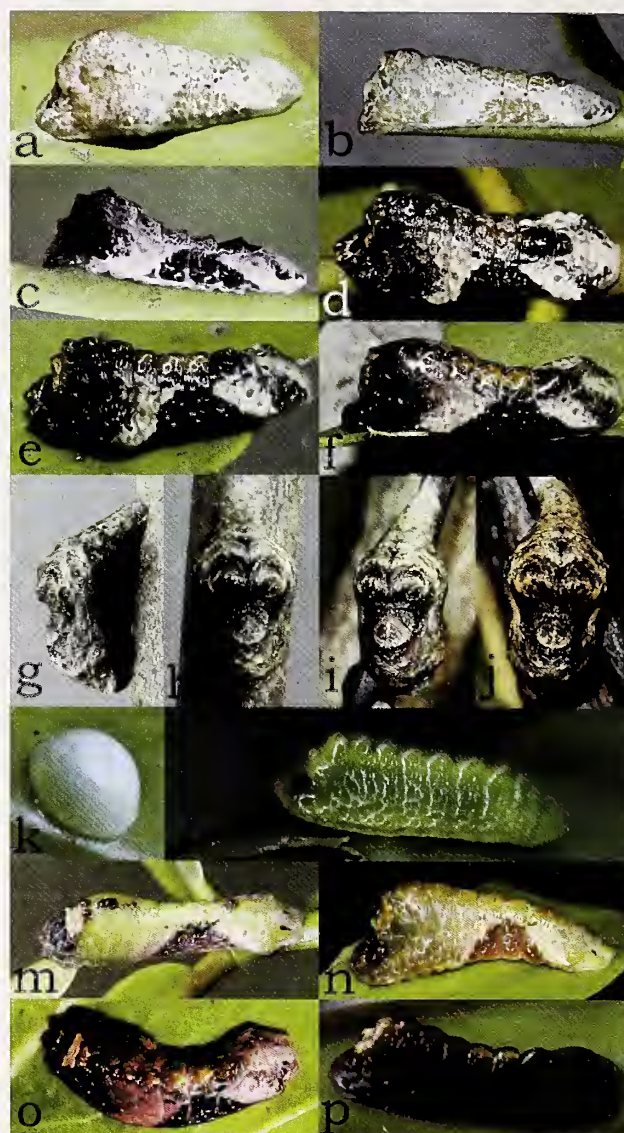


Figure 23. *Tajuria cippus longinus*. a. Larva, fifth instar, off-white form, dorso-lateral view. b. Larva, fifth instar, off-white form, lateral view. c. Larva, fifth instar, light brown form, lateral view. d. Larva, fifth instar, reddish-brown form, dorso-lateral view. e. Larva, fifth instar, dark brown form, dorso-lateral view. f. Larva, fifth instar, dark chocolate brown form, lateral view. g. Pupa, light grayish-green form, lateral view. h. Pupa, light grayish-green form, dorsal view. i. Pupa, brown form with green, dorsal view. j. Pupa, reddish-brown form, dorsal view. k. Egg. l. Larva, third instar, lateral view. m. Larva, fourth instar, light green form, dorso-lateral view. n. Larva, light greenish-brown form, lateral view. o. Larva, light reddish-brown form, dorsal view. p. Larva, dark reddish-brown form, dorso-lateral view.

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BOOK REVIEW

Wild Ones by Jon Mooallem, 2013

Penguin Group, New York, NY. Hardbound, 339 pp. ISBN 978-1-59420-442-5. Price: \$27.95.

As a report on status and trends of the vision of mankind concerning biodiversity issues in the United States, Jon Mooallem has produced a remarkable work. Before proceeding too far, however, I must make a disclaimer that I am one of his characters who contribute to the scene, although not passing through unscathed. Mooallem's approach is through a cast of characters representing a spectrum of participants from politics, public and private conservation organizations, academics, film makers, and deeply involved citizens whose thoughts and actions form most major takes on biodiversity, conservation, systematics, and related issues. For a formally trained journalist and former kosher butcher, his understanding of the scene is a marvel and well beyond that of most of his cast. Mooallem is more than the sum of the parts. A living demonstration that most people capable of critical reasoning could grasp the fundamentals of natural history biology once they can overcome emotion and mysticism. Spirit does nevertheless provide flavor.

His personal underlying motive was to provide his very young daughter with some emotional attachment to the natural world around her - or at least what is left of it - while hopefully developing some sense of its reality compared with the imaginary animal kingdom of the commercial world that engulfs children today. This view includes awareness of drastic changes that will happen during her lifetime. The book is divided into three sections based on three charismatic zoological categories in order: polar bears, butterflies (Lange's metal mark) and birds (whooping crane). These are exemplars of conservation biology principles and how they are playing out in the theater of the changing world.

Three major themes struck me. The first deals with the widespread ignorance that prevents understanding, and thus denial, of climatic change taken as a largely

American phenomenon based on distrust of scientists and science. The fact leaves what is humanity's overwhelming problem not being addressed. Media inattention thus appears the result of a political power equation completely unbalanced in favor of economic expansion at any cost.

Baseline shift is a very real universal phenomenon overlooked by most people because the decline of the all components of the natural world - species, communities and ecosystems sizes and numbers - are masked by the enormous increase and spread of wealth among the top quintile of the human species. Selective memory is universal, so each generation experiences a natural world diminished by the prior generation to which are added further change across each lifetime that is usually incorporated as a new default state. "We paved over paradise to put up a parking lot."

And, these changes are irreversible.

Last, and beyond comprehension of even some biologists, is the relevance of the "species" problem to conservation. Mooallem demonstrates an unusual line of thought in developing his discussion of the endangered species act (ESA) in terms of species concepts. The existential paradox is that species both do and do not exist in terms of the basic textbook (Ernst Mayr) criterion of reproductive isolation. A thorough discussion is not suitable here as paraphrasing the text and even more literature would be necessary. However, note that the guiding principle of all biology is adaptation through evolutionary processes. One by-product of these processes is the occurrence of groups of similar individuals in time and space that humans describe as species. The category is obviously of enormous heuristic value. However, the real concern of biology is to understand the processes of how biodiversity (at all its levels from local breeding populations through ecosystems) is created and maintained. The ESA only attempts to save biodiversity by means of "species." As is so stunningly described in the book, understanding what saving biodiversity really means is so incredibly complex that it is not fully comprehended by most stakeholders who are incapable of overcoming the oversimplification of "species."

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Taxonomic changes in the Neotropical Pericopina and Ctenuchina moths (Erebidae, Arctiinae, Arctiini), with description of new taxa

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Abstract. Thirty four species, belonging to 10 genera are treated; one genus and 53 species names are new synonyms, six are revised synonyms; one new and one revised combinations, and six new and three revised species are established; 11 lectotypes are designated.

Key words: New species, new synonyms, new combinations, new taxa, reviewed distributions.

INTRODUCTION

In the process of gathering material and checking collections to produce a guide to the Pericopina of Mesoamerica and Mexico (Becker, in prep.), a good deal of information important to the guide was accumulated. As such information does not fit in the style of a guide it has to be dealt with separately prior to publication. Some of the information gathered is not related to the fauna of that region, but is important to a better understanding of the group in itself and so is also included. As the adult imagines of all the Mesoamerican and Mexican species will be illustrated in the guide, they are omitted from this work, being presented only if pertinent to taxa not included in that work. For easy access to the information the taxa in this text are arranged in alphabetical order by genus, and the species in alphabetical order under each genus.

Both Pericopina and Ctenuchina had subfamily status before Lafontaine & Fibiger (2006) ranked the Arctiidae as a subfamily of the Erebidae and, consequently, all groups ranked as subfamily or tribe were downgraded to tribe

and subtribe status. Currently the Arctiinae is classified as a member of the Erebidae, a group with family rank, removed from the Noctuidae (Zahiri *et al.*, 2012).

The great number of synonyms is justified by the fact that most Pericopina species are not only highly variable but strongly dimorphic, with sexes being described as different species, often in different genera. As recognized by Lamas & Grados (1996: 22), the current classifications of the group (Hering, 1925; Watson & Goodger, 1986) present ‘... un exagerado número de géneros y especies.’

The material studied in this work is deposited in the following institutions: Natural History Museum, London (BMNH), Carnegie Museum of Natural History, Pittsburgh (CMNH), Instituto Biológico, São Paulo (IBSP); Instituto Nacional de Biodiversidad, Costa Rica (INBio); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museum für Naturkunde der Humboldt-Universität, Berlin (MNHU); University Museum, Oxford (UMO); Instituto de Biología, Universidad Autónoma de México (UNAM); National Museum of Natural History, Washington (USNM); Department of Zoology, Universidade Federal do Paraná, Curitiba (UFPR); and the author's collection (VOB).

Abbreviations follow Anonymous (1978), and Heppner (1984).

NOMENCLATURAL SUMMARY

Arctiini

Ctenuchina

Agyrta Hübner, [1820]

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- dux* (Walker, 1854) (*Diopthis*)
superba (Druce, 1885) (*Isostola*), **syn. rev.**
Coreura Walker, [1865]
phoenicides (Druce, 1884) (*Eucyane*), **comb. n.**
- Pericopina**
- Calodesma* Hübner, [1820]
maculifrons (Walker, [1865]) (*Stenele*)
melanchroia (Boisduval, 1870) (*Cocastria*), **syn. n.**
Chetone Boisduval, 1870
zuleika Becker & Goodger, **sp. n.**
Dysschema Hübner, 1818
amphissum (Geyer, 1832) (*Episteme*)
fenestrata (Walker, 1855) (*Pericopis*), **syn. n.**
vestalis (Butler, 1871) (*Pericopis*), **syn. rev.**
arema (Boisduval, 1870) (*Tebrone*)
imitata (Druce, 1910) (*Pericopis*), **syn. n.**
titan (Druce, 1910) (*Pericopis*), **syn. n.**
boisduvalii (Hoeven, 1840) (*Glaucopis*)
principalis (Jørgensen, 1935) (*Pericopis*), **syn. n.**
regalis (Jørgensen, 1935) (*Pericopis*), **syn. n.**
rubripicta (Butler, 1872) (*Pericopis*), **syn. n.**
trapeziata (Walker, 1854) (*Daritis*), **syn. n.**
trapeziata; (Hering, 1925) (*Pericopis*), [*partim*, female
woodii (Butler, 1867) (*Mazaeras*), **syn. n.**
centenarium (Burmeister, 1879) (*Eucharia*)
jaonis (Strand, 1911) (*Pericopis*), **syn. rev.**
eurocilia (Cramer, 1777) (*Phalaena*)
amadema (Druce, 1907) (*Pericopis*), **syn. n.**
aorsa (Boisduval, 1870) (*Chetone*), **syn. n.**
bivittata (Walker, 1854) (*Pericopis*), **syn. n.**
daphne (Druce, 1885) (*Pericopis*), **syn. n.**
disjuncta (Walker, 1856) (*Pericopis*), **syn. n.**
flavimedia (Monte, 1933) (*Pericopis*), **syn. n.**
fulgorata (Butler, 1871) (*Pericopis*), **syn. n.**
hypoxantha Hübner, 1818, **syn. n.**
leonina (Butler, 1872) (*Pericopis*), **syn. n.**
leptoptera (Perty, [1833]) (*Sericaria*), **syn. n.**
molesta (Hering, 1925) (*Pericopis*), **syn. n.**
nigrivenata (Hering, 1925) (*Pericopis*), **syn. n.**
parviflava (Hering, 1926) (*Pericopis*), **syn. n.**
postflava (Hering, 1926) (*Pericopis*), **syn. n.**
sibylla (Butler, 1873) (*Pericopis*), **syn. n.**
unxia (Druce, 1910) (*Pericopis*), **syn. n.**
fantasma (Butler, 1873) (*Pericopis*)
innominatum Becker, **sp. n.**
trapeziata; (Hering, 1925) (*Pericopis*), [*partim*, male],
misid.
forbesi (Druce, 1907) (*Pericopis*)
evanescens (Hering, 1925) (*Pericopis*), **syn. n.**
hilarum (Weymer, 1895) (*Thebrone*)
biformis (Schaus, 1901) (*Pericopis*), **syn. n.**
hilarina (Weymer, 1914) (*Thebrone*), **syn. n.**
*hilarina*f. *fulva* (Weymer, 1914) (*Thebrone*), **syn. n.**
intermedium Becker, **sp. n.**
- leda* (Druce, 1884) (*Pericopis*)
paracelsus (Hering, 1926) (*Pericopis*), **syn. n.**
luctuosum (Dognin, 1919) (*Pericopis*)
aethiops (Hering, 1928) (*Pericopis*), **syn. n.**
lygdamis (Druce, 1884) (*Pericopis*), **stat. rev.**
fortis (Schaus, 1910) (*Pericopis*), **syn. n.**
*marginalis*f. *tibexina* (Hering, 1930) (*Pericopis*), **syn. n.**
ultima (Hering, 1926) (*Pericopis*), **syn. n.**
viduopsis (Hering, 1926) (*Pericopis*), **syn. n.**
mariamne (Geyer, [1838]) (*Eucharia*), **stat. rev.**
fenestrata (Butler, 1872) (*Pericopis*), **syn. n.**
minor Becker, **sp. n.**
perplexum (Schaus, 1910) (*Pericopis*)
guapa (Schaus, 1910) (*Pericopis*), **syn. n.**
pictum (Guérin-Méneville, [1844]) (*Callimorpha*)
*indecis*a (Walker, 1854) (*Pericopis*), **syn. rev.**
lucifer (Butler, 1873) (*Pericopis*), **syn. rev.**
subapicalis (Walker, 1854) (*Pericopis*)
pagasa (Dognin, 1919) (*Pericopis*), **syn. n.**
thetis (Klug, 1836) (*Euprepia*)
howardi (Edwards, 1887) (*Daritis*), **syn. n.**
thyridinum (Butler, 1871) (*Pericopis*)
damon (Druce, 1910) (*Pericopis*), **syn. n.**
grassator (Hering, 1925) (*Pericopis*), **syn. n.**
mosera (Druce, 1907) (*Pericopis*), **syn. n.**
sylvia (Druce, 1910) (*Pericopis*), **syn. n.**
talboti (Dognin, 1922) (*Pericopis*), **syn. n.**
viuda (Schaus, 1910) (*Pericopis*)
joiceyi (Dognin, 1923) (*Centronia*), **syn. n.**
- Hypocrita* Hübner, 1807
celina (Boisduval, 1870) (*Calepidos*)
escuintla (Schaus, 1920) (*Eucyane*), **syn. n.**
- Josiomorpha* Felder, 1874
cathetozosta Becker, **sp. n.**
triangulifera Hering, 1925, **stat. rev.**
- Phaloe* Guérin-Méneville, [1838]
Sphaeromachia Grote, 1877, **syn. rev.**
cubana (Herich-Schäffer, 1876) (*Pericopis*), **comb. rev.**
gaumeri (Druce, 1884) (*Phaloe*), **syn. n.**
- Phaloesia* Walker, 1854
saucia Walker, 1854
fulvicolis Butler, 1876, **syn. rev.**
flaviventris Reich, 1938, **syn. n.**
- Pseudophaloe* Hering, 1925
ninonia (Druce, 1884) (*Eucyane*)
cotta (Druce, 1897) (*Pericopis*), **syn. n.**
levisi (Schaus, 1910) (*Phaloe*), **syn. n.**
promiscua Becker, **sp. n.**
schausi (Edwards, 1884) (*Pericopis*)
verania (Druce, 1884) (*Phaloe*), **syn. n.**
veranioides Hering, 1925, **syn. n.**
- Sermyla* Walker, 1854
transversa Walker, 1854
morta Schaus, 1892, **syn. n.**

TAXONOMY

Ctenuchina

Agyrtia dux (Walker)

Dioptis dux Walker, 1854: 327. Holotype ♀, VENEZUELA: [no further data] (BMNH) [not examined].

Isostola superba Druce, 1885: 115. Holotype ♂, GUATEMALA: Verapaz, Teleman (*Champion*) (BMNH) [not examined]. **Syn. rev.**

Remarks. *I. superba* is a Ctenuchina that Hampson (1898: 470, fig. 257) had already synonymized with *A. dux*, along with *A. aestiva* Butler, and *A. phyla* Druce, a treatment followed by Draudt (1915: 162, pl. 24a). The figures presented by both Hampson and Draudt match the excellent colour illustration of *superba* in Druce (1884: pl. 12, fig. 5). Both Hering (1925: 434) and Watson & Goodger (1986: 34) overlooked this synonymy and included *I. superba* again in the Pericopinae.

Coreura phoenicides (Druce), **comb. n.**

Eucyane phoenicides Druce, 1884: 105. Holotype ♂, GUATEMALA: Coban (MNHU) [not examined].

Remarks. The illustration in Druce (1884: pl. 10, fig. 15), clearly shows that this species is closely related to other species in this Ctenuchina genus, such as *C. fida* (Hübner), *C. lysimachides* Druce, and *C. albicosta* Draudt, and very likely the last is a synonym of it. The name *E. phoenicides* was overlooked in all major works subsequent to Kirby (1892: 189).

Pericopina

Calodesma maculifrons (Walker)

Stenele maculifrons Walker, [1865]: 157. Holotype ♂, [HONDURAS]: Limas (BMNH) [examined].

Cocastromelanchroia Boisduval, 1870: 88. Holotype ♀, GUATEMALA: [No further data] (BMNH) [image examined]. **Syn. n.**

Remarks. A strongly dimorphic species with males having yellow or orange ground colour [*maculifrons*], whereas females have it black [*melanchroia*]. Several specimens were reared on several species of Malpighiaceae in Costa Rica (Janzen & Hallwachs, 2013), making possible the association of sexes. This is another example of the importance of rearing adults from immatures in order to clarify such questions.

Chetone zuleika Becker & Goodger, **sp. n.**

Pericopis ithomia; Hering, 1925: 438 (partim), pl. 62a.

Diagnosis. Very similar to *C. ithomia* (Boisduval), and often found mixed with this in the collections. In *C. ithomia* the dots

on thorax are small and white, and the series of yellow marks that form the first oblique fascia across of forewings starts before the middle of costa, as illustrated in Felder (1874: pl. 103, fig. 7), whereas in *C. zuleika* the dots on thorax are orange and larger, and the marks that composes the first fascia starts about half way of costa, as illustrated in Hering (1925, pl. 62a). Also the black margin of hind wings, in *C. ithomia* is broader, with internal edge irregular, whereas in *C. zuleika* it is narrower, with the internal edge more regular.

Material studied (10 ♂♂, 9 ♀♀). Holotype ♀, PANAMA: Taboga Is., 10.vi.1911 (*Busck*) (USNM). Paratypes: ♂ PANAMA: Bugaba [no further data]; ♂, Panama (Bro. *Regis* Col.) [no further data]; ♂, C[anal] Z[one], La Pita, 13.xi.1963 (*Small*); ♀, C[anal] Z[one], Cocoli, 27.vi.1963 [(*Small*)]; ♀, Panama, El Llano, Cordillera de San Blas, 330 m, vi.1978 (*Small*); ♀, Veraguas, Santa Fe, 230 m, 20.ix.1975 (*Small*); ♂, [no data] (ex *Schaus* Col.); ♂, “775” [no further data] (ex *Schaus* Col.); ♂, “605” [no further data] (ex *Schaus* Col.); ♀, “605” [no further data] (ex *Schaus* Col.) (USNM); ♀, [?]: [No data] (CMNH); 2 ♂♂, 2 ♀♀, Chiriqui [no further data] (ex *Staudinger* Col., ex *Rothschild* Col.) (BMNH); ♂, COLOMBIA: [No further data] (BMNH); ♂, BRAZIL: [No further data] [mislabelled?] (BMNH); ♀, [No data]: “156 *Rothschild* Bequest BM 1939-1” (BMNH).

Etymology. Name of women; after *Heliconius hecale zuleika* Hewitson, one of its mimics.

Remarks. This and *C. ithomia* are perfect mimics of the butterflies *Heliconius hecale zuleika* Hewitson, *Tithorea tarricina pinthias* Godman & Salvin, and *Eueides procula vulgiformis* Butler & Druce (Nymphalidae), and of *Papilio ascolius zalates* Godman & Salvin (Papilionidae).

Dysschema amphissum (Geyer)

Episteme amphissum Geyer, 1832: 35. Type (s) ♀, BRAZIL: [No further data] [lost].

Coborisa fenestrata Walker, 1855: 915. Lectotype ♂, [BRAZIL: RJ] ‘Mexico?’ (BMNH), here designated [image examined]. **Syn. n.**

Pericopis vestalis Butler, 1871: 289. Holotype ♂, BRAZIL: [RJ] [No further data] (UMO) [image examined]. **Syn. rev.**

Remarks. The two male syntypes of *C. fenestrata* are descaled, mislabeled specimens. The specimen bearing the following labels is here selected as the lectotype: round, red edged ‘Type’; round, blue edged ‘Syntype’; long, white, printed ‘1. Coborisa fenestrata’; round, white ‘43, 58’; the second bearing the following labels, is designated as paralectotype: round, blue edged ‘Syntype’; round, white ‘43, 58’, long, white, typed ‘fenestrata Walker.’ The species is known only from Southeastern Brazil. In VOB there is a large series of specimens ranging from Southern Minas Gerais and Rio de Janeiro, south to Rio Grande do Sul. The males show some variation both in the shape of the forewings and in the intensity of scaling. Some individuals have slightly narrow, more pointed forewings, matching the syntypes of *fenestrata* and the holotype of *vestalis*, whereas others have them more

rounded, with margins and two oblique, faint gray bands from costa to dorsum and termen respectively, as shown in Hering (1925: pl. 64b). The last had been synonymized under *amphissa* (Hering, 1925: 443), but listed as valid species by Watson & Goodger (1986: 38). The male genitalia of all forms are identical. As with other species of the genus, males are commonly attracted to light, whereas the females are diurnal, resembling nymphalid and papilionid butterflies. In the case of *D. amphissum* females mimic *Actinotes* species. In the author's personal copy of Seitz's work, purchased from the heirs of J. Zikán, there is a pencil note, in his handwriting, next to *P. fenestrata*, stating: 'F.[azenda] d.[os] C.[ampos]' ♂, ♀, r.[eared] on assa-peixe [*Vernonia* sp., Asteraceae]. According to O. Mielke (pers. comm.) this place is located in Virginia, state of Minas Gerais, next to the border with Rio de Janeiro.

Dysschema arema (Boisduval)

Tebrome arema Boisduval, 1870: 85. Holotype ♂, COLOMBIA: [No further data] (BMNH) [image examined].

Pericopis imitata Druce, 1910: 170. Holotype ♂, PERU: Limbani, Carabaya, v.1904 (*Ockenden*) (BMNH) [image examined]. **Syn. n.**

Pericopis titan Druce, 1910: 170. Holotype ♀, PERU: Chanchamayo (*Watkins*) (BMNH) [image examined]. **Syn. n.**

Remarks. The males show some variation in pattern, especially in the hind wings. Some specimens have the external band reaching the cell, as in the type of *arema*; others have a band beyond the cell, followed by pair of light dots as in *imitata* and *titan*. The author collected a series in Ecuador that represents both forms.

Dysschema boisduvalii (Hoeven)

Figs. 1-3

Glaucopis boisduvalii Hoeven, 1840: 279. Syntype? ♂, BRAZIL [no further data] (BMNH) [image examined].

Arctia funeralis Herrich-Schäffer, [1856]: pl. 92, fig. 527. Syntype? ♂, [no further data] [S. America] (BMNH) [image examined]. Synonymized by Herrich-Schäffer [1858]: 84.

Pericopis principalis Jörgensen, 1935: 119. Holotype ♀, PARAGUAY: Trinidad (*Schade*) [lost]. **Syn. n.**

Pericopis regalis Jörgensen, 1935: 117, pl. 4, fig. 27. Holotype ♀, ARGENTINA: "Guaycoléc. Territorio de Formosa" (*Jörgensen*) [MACN] [not examined]. **Syn. n.**

Pericopis rubripicta Butler, 1872a: 50. Holotype ♀, [COLOMBIA]: Bogota (UMO) [image examined]. **Syn. n.**

Daritis trapeziata Walker, 1865: 281. Holotype ♀, "In Mr Norris's collection" [no further data] [South America] [lost]. **Syn. n.**

Mazaeras woodii Butler, 1867: 218, pl. 4, figs. 2, 3. Holotype ♀, [BRAZIL]: Bahia (Col. Wood) [lost]. **Syn. n.**

Pericopis trapeziata; Hering, 1925: 427, pl. 60c [*partim*, female].

Remarks. A series of males and females (VOB 56051) was reared by the author from a single brood of caterpillars found feeding on leaves of *Vernonia* sp. (Asteraceae).

The sexes are strongly dimorphic. Males, described twice, are white with four blackish dots on forewings (Fig. 2), matching the illustrations of *A. funeralis* in Herrich-Schäffer, and of *boisduvalii* in Hering (1925: pl. 60c), as well as specimens labeled '*Glaucopis Boisduvalii* Van der Hoeven' 'Syntype?' and '*Arctia funeralis* Herr. S. Brèsil' 'Syntype?' in the BMNH. Both specimens bear a round, blue edged labels 'Syntype', with question marks. For this reason and by the fact that other specimens might be found in other collections, no lectotype designations are proposed. The females, described five times, are mostly blackish with the dots on abdomen reduced (Figs. 1, 3), matching the original descriptions of *trapeziata* and *woodii* and the descriptions, illustration and the type material of *rubripicta*, *regalis* and *principalis*. Hering (1925: 427, pl. 60c) correctly synonymized *rubripicta* and *woodii* under *trapeziata* but wrongly associated it to the males of an unnamed species from Southern Brazil (see *innominatum* below). The figure of the type of *regalis* in Jörgensen (1935: pl. 4, fig. 27) leaves no doubt that it is a female of *boisduvalii*, and the original description of his *principalis* matches a form with reduced pattern, also represented in the series reared by the author. According to him (Jörgensen 1935: 119): "(Como el ejemplar típico [of *principalis*] ha desaparecido, la descripción anterior incompleta está hecha según la acuarela del señor Schade)." The types of both *D. trapeziata* and *M. woodii*, supposedly in the BMNH or UMO, were not traced. In the BMNH there are manuscript notes by G. Hampson stating that the specimens belonging to both Norris and Wood collections were returned to the owners and are presumably lost.

Dysschema centenarium (Burmeister)

Figs. 5, 6, 17

Eucharia centenaria Burmeister, 1879: 436. Type ♂, ARGENTINA: [not examined].

Pericopis jaonis Strand, 1911: 77; 1914: 9, pl. 4, fig. 20; Hering, 1925: 428, pl. 60g. Holotype ♀, BRAZIL: [RS?], São João (BMNH) [image examined]. **Syn. rev.**

Remarks. *D. centenarium* ranges from Argentina and Uruguay to southern Rio Grande do Sul State, and has been reared several times on the leaves of *Eryngium paniculatum* (Apiaceae) in Uruguay (Achaval 1968: 102), and on *E. eburneum* in Argentina (Jörgensen 1935: 117). One of the females obtained from such rearings is in VOB (presented by the late Prof. Biezanko). This female matches exactly the type of *jaonis*, a name that had already been synonymized under *centenaria* by Jörgensen (1935: 117), an action overlooked by Watson & Goodger (1986: 38), who listed them as different species.

Dysschema eurocilia (Cramer)

Phalaena eurocilia Cramer, 1777: 148, pl. 178, C. Type(s) ♀, [SURINAM]: "Antilles", no further data [not examined] [lost?].

Pericopis anadema Druce, 1907: 300. Holotype ♂, COLOMBIA: Minca, 2000 ft. (Smith) [image examined]. **Syn. n.**

Chetone aorsa Boisdual, 1870: 90. Holotype ♀, GUATEMALA: [No further data] (BMNH) [image examined]. **Syn. n.**

Pericopis bivittata Walker, 1854: 348. Holotype ♀, VENEZUELA: [No further data] (BMNH) [image examined]. **Syn. n.**

Pericopis daphne Druce, 1885: 113. Holotype ♀, PANAMA: San Juan (Ribbe) (MNHU) [image examined]. **Syn. n.**

Pericopis disjuncta Walker, 1856: 1655. Holotype ♀, COLOMBIA: [No further data] (UMO) [image examined]. **Syn. n.**

Pericopis flavimedia Monte, 1933: 30. Lectotype ♀, [BRAZIL: MG, Belo Horizonte] (Monte) (IBSP), here designated [not examined]. **Syn. n.**

Pericopis fulgorata Butler, 1871: 287. Holotype ♀, [BRAZIL: PA, Belém, 'Para' (UMO) [image examined]. **Syn. n.**

Pericopis heliconissa Strand, 1921: 126. Holotype ♀, PERU. Synonymized by Lamas & Grados, 1986: 25.

Pericopis hodeva Druce, 1910: 173. Holotype ♀, PERU: [Pasco], Pozuzo (BMNH) [image examined]. Synonymized by Lamas & Grados, 1996: 25.

Dysschema hypoxantha Hübner, 1818: 31, pl. [34], figs. 191, 192. Type ♂, SURINAM: [No further data] [lost?]. **Syn. n.**

Pericopis leonina Butler, 1872b: 89. Holotype ♀, COSTA RICA: [No further data] (BMNH) [image examined]. **Syn. n.**

Sericaria leptoptera Perty, [1833]: 160. Type ♀, [BRAZIL: PA] ['Amazonum flumen'] [lost?]. **Syn. n.**

Pericopis lucretia Butler, 1876a: 340. Holotype ♀, [COLOMBIA: Cundinamarca], Veragua '75-28' (BMNH) [image examined]. Synonymized by Hering, 1925: 442.

Pericopis eurocilia f. *melaina* Hering, 1925: 443. Holotype ♀, VENEZUELA: Tachira (Briceño) (BMNH) [image examined].

Pericopis molesta Hering, 1925: 443. Holotype ♂, COLOMBIA: Popayan, 1895 (Kalbreyer) (MNHU) [image examined]. **Syn. n.**

Pericopis nigrirenata Hering, 1925: 439. Holotype ♂, ECUADOR: Los Llanos, 1400 m (MNHU) [image examined]. **Syn. n.**

Pericopis eurocilia f. *obscurata* Hering, 1925: 443. Holotype ♀, PERU: Chanchamayo (Thamm) (MNHU) [image examined].

Pericopis parviflava Hering, 1926: 132. Holotype ♂, ECUADOR: [No further data] [image examined]. **Syn. n.**

Pericopis postflava Hering, 1926: 132. Holotype ♂, COLOMBIA: Villavicencio (Fassl) (MNHU) [image examined]. **Syn. n.**

Pericopis recta Hering, 1925: 442. Holotype ♀, COLOMBIA: Cauca (Patiño) (MNHU) [image examined]. **Syn. n.**

Pericopis rhea Druce, 1910: 174. Holotype ♀, PERU: [No further data] (BMNH) [image examined]. Synonymized by Lamas & Grados, 1996: 25.

Pericopis irene f. *splendidissima* Hering, 1925: 443. Holotype ♀, PERU: [Puno], Santo Domingo, Carabaya, 6000 ft, vi.1901 (Ockenden) (BMNH) [image examined]. Synonymized by Lamas & Grados, 1996: 25.

Pericopis staudingeri Druce, 1910: 174. Holotype ♀, PERU: Cuzco (BMNH) [image examined]. Synonymized by Watson & Goodger, 1986: 38.

Pericopis sibylla Butler, 1873: 127. Holotype ♂, [BRAZIL: ES], 'Esp. San.', [No further data], (UMO) [image examined]. **Syn. n.**

Pericopis umbra Druce, 1885: 113. Holotype ♀, [EL] SALVADOR: S. Salvador (MNHU) [image examined]. **Syn. n.**

Pericopis unxia Druce, 1910: 175. Holotype ♂, PERU: [Puno], La Union, Rio Huacamayo, Carabaya, 2000 ft, xi, xii.1904 (Ockenden) (BMNH) [image examined]. **Syn. n.**

Phalaena zerbina Stoll, 1790: 184. Type(s) ♀, SURINAM: [No further data] [not examined] [lost?]. Synonymized by Hering, 1925: 423.

Remarks. This is a common species throughout Tropical America and highly variable, especially the females of which two specimens that looks exactly alike are rarely found. As can be seen above, most of the names have been regarded as forms or subspecies of either *eurocilia* or *hypoxantha*. However, as the species has continuous distribution and the different forms are connected to each other by intermediate forms, they cannot be considered as subspecies. The figure of *S. leptoptera* in Perty ([1833]: pl. 32, fig. 3) clearly indicates that the specimen he described is the female of form *hypoxantha*. The type material of *P. melini* Bryk, 1953, were not examined, however, it has also been synonymized with *D. hypoxantha* (Watson & Goodger, 1986: 38). *P. flavimedia* was synonymized with *D. hypoxantha* by Lima (1936: 258), following a personal communication by Travassos, a concept followed by subsequent authors (Silva *et al.*, 1968; Mielke & Casagrande, 1999), but apparently overlooked by Watson & Goodger, 1986), who maintained it as a valid species. According to the original description and the excellent figure of the lectotype in Mielke & Casagrande (1999: 229, fig. 5), there is no doubt that this is another junior synonym of *D. eurocilia*. Monte, in the original description, was correct to point out that *flavimedia* is closely related to *D. irene* (Druce), also one of the synonyms of *D. eurocilia* (Lamas & Grados, 1996). Mielke & Casagrande (1999: 229) wrongly stated that the specimen in the IBSP is the holotype. According to the original description, Monte stated that he kept at least five of the specimens reared from caterpillars, feeding on the leaves of *Vernonia* sp. (Asteraceae), and Lima (1936: 258) mentioned that he was informed by Travassos that one "cotype" was in the old Instituto de Biologia Vegetal, Rio de Janeiro. The specimen studied by Mielke & Casagrande is here designated as the lectotype. A. Aiello provided a photograph of a male, which matches the type of *molesta*, reared on *Lepidaploa canescens* (Asteraceae), in Panama. Watson & Goodger (1986: 37) wrongly cited '[C. America]' as the type locality of *P. lucretia*.

Dysschema fantasma (Butler)

Fig. 12

Pericopis fantasma Butler, 1873: 126. Lectotype ♂, [BRAZIL: 'Colombia': No further data (UMO), here designated [image examined].

Remarks. The type-locality seems incorrect as all specimens deposited in the BMNH, USNM, CMNH, and in VOB, came from Southeastern Brazil. There are two males in the UMO, with identical data, labeled

'type.' The specimen bearing a white, rectangular label stating 'Type Lep. 363, 1/2, *Pericopis fantasma* Butler, HOPE DEPT. OXFORD' is here selected as the lectotype. In Zikán & Zikán (1968: 80), *D. terminata* (Guérin-Méneville) is listed as the female of this though with no justification [reared?] what is possible as both are known by their opposite sexes only. If true the last name has priority.

Dysschema forbesi (Druce)

Pericopis forbesi Druce, 1907: 301. Holotype ♀, BRAZIL: [SC], Quipapa (*Forbes*) (BMNH) [image examined].

Pericopis evanescens Hering, 1925: 440. Holotype ♂, BRAZIL: SP, Casa Branca, 1890 (*Garbe*) (MNHU) [image examined]. **Syn. n.**

Remarks. The colour pattern and distribution indicate that the types represent the opposite sex of the same species.

Dysschema hilarum (Weymer)

Thebrone hilara Weymer, 1895: 325. Holotype ♀, BRAZIL: RS 'Rio Grande do Sul', (MNHU) [image examined].

Pericopis biformis Schaus, 1901: 269. Lectotype ♂, BRAZIL: PR, Castro (USNM), here designated [examined]. **Syn. n.**

Thebrone hilarina Weymer, 1914: 7. Type ♀, BRAZIL: [utatele] (BMNH) [image examined]. **Syn. n.**

Thebrone hilarina f. fulva Weymer, 1914: 7. BRAZIL: [No further data] (MNHU) [not examined]. **Syn. n.**

Pericopis hilara f. mutata Hering, 1925: 441. BRAZIL: PR, Castro (*Jones*) (BMNH) [image examined].

Remarks. This is a variable species, with the ground colour of hind wings pale yellow to purple, or nearly all brown in the females, as the case in *hilara*'s type specimen and *biformis*' female paralectotype, to almost totally blackish as in the type of *mutata*.

Dysschema innominatum Becker, **sp. n.**

Figs. 4, 8, 15, 16

Pericopis trapeziata; Hering, 1925: 427, pl. 60c [*partim*, male], misid.

Daritis trapeziata; Zikán & Zikán, 1968: 80, misid.

Diagnosis. Very similar to *D. centenarium*, both externally and in the shape of male genitalia. It can be readily distinguished by the pattern of its hind wings: it has a red, black bordered mark outside the end of cell—absent in *centenarium*. The expansion of the sacculus vestigial, about ¼ of that of costa—half the size in *centenarium*.

Description. Male forewings 22–25 mm. Head—including palpi and antennae—and thorax black. Patagia and base of tegulae white. Legs black; tarsi with sparse white scales. Wings translucent white; cilia white. Forewings with black pattern as follows: costa, above cell; oblong patch on mid cell; sub triangular patch at end of cell, connected to costa; broad triangle at apex, from distal fourth of costa to mid termen; triangle on termen, above tornus, with vertex half way between M_3 and Cu_1 ; dorsum black, finely bordered white, not reaching tornus. Hind wings bordered black

with enclosed white dots between cells, bordered red internally; red, bordered black dot at end of cell. Abdomen striped black and white longitudinally.

Genitalia ♂. Socii long, branching V-shape, arms slightly incurved distally, covered dorsally with sparse, long setae. Vinculum a narrow belt slightly incurved basally. Juxta H-shaped. Valvae twice as long as broad; tip of sacculus vestigial. Aedoeagus sinuous; basal half oval; distal half tubular, ending in a long, sharp tooth; small, sharp thorn before apex, ventrally.

Female. Pattern similar to that of male, but with light areas dusted gray, not white; basal half of hind wings black.

Material studied (17 ♂♂, 1 ♀, 2 male genitalia slides). Holotype ♂, BRAZIL: SP, Campos do Jordão, 22°46' S, 45°31' W, 1600 m, 23–27.i.2001 (*Becker*, 131020) (UFPR); paratypes: 3 ♂♂, same data as holotype; 2 ♂♂, RJ: Itatiaia, 2300, 26.i.1993 (*Becker*, 86.494); 4 ♂♂, SC, São Joaquim, 1400 m, 2.ii.1993 (*Becker*, 87601); 2 ♂♂, SC, Urubici, Serra do Panelão, 1300 m, 14–17.ii.2007 (*Moser*); ♂, SC, Curitiba, 1000 m, 17.ii.2008 (*Moser*); ♀, PR, Serra do Itararé, 1000 m, 7–8.ii.2008 (*C. G. Mielke*), flying at day time; ♂, RS, Garibaldi, 9.iii.1967 (*Becker*, 3817); 4 ♂♂, RS: São José dos Ausentes, 1200 m, 28–31.i.2000 (*Silveira*); 2 ♂♂, São Francisco de Paula, Rio Sta. Cruz, 650 m, 24.i.2006 (*Moser*).

Etymology. From the Latin 'innominatus' = nameless.

Remarks. The species described and illustrated by Hering (1925: 427, pl. 60c) as *trapeziata* had the sexes wrongly associated, belonging to two different species: the female to *boisduvalii* (see above); the male to an undescribed species. The other evidence that does not support Hering's proposal is distribution: *boisduvalii* ranges from southern Brazil and Paraguay up to Bogota, in Colombia; the undescribed, represented by the male, is restricted to Southern Brazil, ranging from Northern Rio Grande do Sul State, to the mountains of Rio de Janeiro.

Dysschema intermedium Becker, **sp. n.**

Fig. 13

Diagnosis. Intermediate between *D. magdala* and *D. gaumeri*. In *magdala* the basal half of fore wings is homogeneous gray, with no white mark near thorax, and no white dots along margins; the hind wings have only a trace of a line at the end of cell whereas in *intermedium* this line is strongly developed. *D. gaumeri* has the pattern more reduced and the dark gray band along the hind wing margins is reduced to a series of dots on veins.

Description. Male forewings 35 mm. Head and thorax black; tegulae with a broad yellow band frontally. Legs yellow ventrally, tibiae and tarsi black. Wings translucent with irregular dark gray areas dusted ferruginous underneath. Fore wings with a diffuse white streak basally connecting with the yellow band on tegulae; costa dark gray interrupted with diffuse whitish for some extension above end of cell and before apex; basal half of cell dusted gray; broad dark gray mark at end of cell, expanding to costa; termen dark gray with a series of small white dots between veins following margin; dorsum gray below 1A, from base to before tornus. Hind wings with costa gray, dusted reddish; termen with irregular reddish band bordered dark gray, sometimes reduced to irregular reddish dots between veins; series of white dots along margin; internal margin covered with sparse, long, dark gray scales; a broad dark gray band at end of cell. Abdomen red with a wide black band dorsally; yellow ventrally.

Female forewings 37–40 mm. Body as in males. Fore wings dark

gray with light areas whitish, dusted gray, instead of translucent. Hind wings orange red; markings similar to those on males.

Genitalia ♂. Similar to those of *D. minor*, [see that] but with socii nearly straight and the expansion of dorsal margin longer and thicker. Aedoeagus also more curved.

Material studied (8 ♂♂, 4 ♀♀, 2 ♂♂ genitalia slides). Holotype ♂, GUATEMALA: Baja Verapaz, Purulha, 1620 m, 20.vii.2000 (*Becker*) (VOB 123199) (USNM); paratypes: 1 ♂, 1 ♀, same data as holotype; 3 ♂♂, 1 ♀, Quetzaltenango, Aguas Georginas, 2500 m, 12.vii.2000 (*Becker*) (VOB 122887); 1 ♂, San Marcos, San Marcos, 2800 m, 9.vii.2000 (VOB 122767); 1 ♂, 2 ♀♀, MEXICO: Chia, San Cristóbal de las Casas, 2300 m, 23-27.vii.1981 (*Becker*) (VOB 43634).

Etymology. From the Latin 'intermedium' = intermediate.

Remarks. The specimens from San Marcos and Aguas Georginas are slightly smaller; the female has hind wings tinged gray basally.

Dysschema leda (Druce)

Pericopis leda Druce, 1884: 111, pl. 11, fig. 13. Holotype ♂, COSTA RICA: [Cartago], [Volcan] Irazu, 6-7000 ft (*Rogers*) (BMNH) [image examined].

Pericopis paracelsus Hering, 1926: 133. Holotype ♂, COSTA RICA: [Cartago], Vulcan Irazu, 1200m (*Fassl*) (MNHU) [image examined]. **Syn. n.**

Remarks. The large series of specimens examined in the several collections studied, that match the type image, indicates that there is only one species that, as Hering pointed out, is "Äusserlich einer marginalis-Rasse ähnlich, aber Hlb oben schwarz, mit zwei gelblich-grauen Subdorsalstreifen, Analbusch rot." Hering (1925: 442) treated *P. leda* as a form of *P. marginalis*, together with *P. magdala* and its forms. It seems that he had no specimen of *P. leda* at that time as the difference in the colour of abdomen between them is striking: dark gray with two sub dorsal yellowish bands in *P. leda*, but red with a black dorsal line in *P. marginalis-magdala*-group. This perhaps is the reason why he described it again as *P. paracelsus*.

Dysschema luctuosum (Dognin)

Figs. 7, 9

Pericopis luctuosa Dognin, 1919: 4. Holotype ♂, [BRAZIL] 'PERU': [No further data] (USNM) [examined].

Pericopis aethiops Hering, 1928: 270. Holotype ♀, BRAZIL: 'Süd Brasil.' (MNHU) [image examined]. **Syn. n.**

Remarks. The type-locality of *P. luctuosa*: "Peru," is presumably a mislabeling as all the specimens examined were collected along the southeastern coast of Brazil, from Rio de Janeiro to Santa Catarina and Lamas & Grados (1996: 23) listed the name, stating that no specimen had been collected in Peru. Male hind wings have two forms: melanic and with ground colour white (the male genitalia of both are identical).

Dysschema lygdamis (Druce), **stat. rev.**

Pericopis lygdamis Druce, 1884: 111. Holotype ♂, COSTA RICA: Irazu, 6-7000 ft (*Rogers*) (BMNH) [examined].

Pericopis fortis Schaus, 1910: 208. Holotype, ♂, COSTA RICA: Tuis, vi. 1907 (Schaus) (USNM), here designated [examined]. **Syn. n.**

Pericopis marginalis f. *tibesina* Hering, 1930: 517. Holotype ♂, COSTA RICA: [No further data] (*Fassl*) (MNHU) [image examined]. **Syn. n.**

Pericopis ultima Hering, 1926: 131. Holotype ♂, PANAMA: Lino (*Fassl*) (MNHU) [image examined]. **Syn. n.**

Pericopis viduopsis Hering, 1926: 132. Holotype ♂, PANAMA: Lino (*Fassl*) (MNHU) [image examined]. **Syn. n.**

Remarks. This species is similar to *D. magdala* but can be easily distinguished by the presence of a short yellow dash at base of forewings. In males the hind wings can vary from nearly translucent whitish [as in the types of *lygdamis*, *fortis* and *tibesina*] to scaled orange [as in the types of *ultima* and *viduopsis*]. In VOB there is a series from Tapanti, Costa Rica, collected on the same sheet at the same night, representing both the extreme as well as intermediate forms. It seems restricted to the mountains of Costa Rica and Panama.

Dysschema mariamne (Geyer), **stat. rev.**

Eucharia mariamne Geyer, [1838]: pl. [47]. Type [s] ?, MEXICO: [No further data] [lost].

Pericopis mariamne f. *fenestrata* Butler, 1872b: 50. Holotype ♂, [GUATEMALA]: San Geronimo (UMO) [image examined]. **Syn. n.**

Remarks. This species has been considered a synonym of *D. thetis* (Hering, 1925: 427, Watson & Goodger, 1986: 38, Lamas & Grados, 1996:25). Two distinct populations are involved here: one, ranging from Southwestern USA and Northwestern Mexico, which has the forewings underside tinged dark gray, known as *D. howardi*, and another, from Eastern Mexico down to Panama, with forewings underside tinged orange, known as *thetis*. However the lectotype of *thetis* belongs to the first population [see *thetis* below], whereas *mariamne* belongs to the second, as clearly shown in the original illustration. Their genitalia show no difference, so it is very likely that both populations belong to one species. However, as they have been regarded as different species (Franclemont, 1984: 114), and further studies are needed to elucidate their status, they are maintained here as distinct. Some confusion is involved with the original illustrations of *mariamne*: as the original plate is not numbered, Watson, Fletcher & Nye (1980: 50) mention 'pl. [46],' and Watson & Goodger (1986: 380) 'pl. [47].' Also, in the facsimile edition by Kirby (1908-1912), the names are transposed: the species illustrated in 'Tafel 485 (47)' as

'*Eucharia Mariamne*' is '*Estigmene lactinea*,' whereas the one illustrated in 'Tafel 486(48)' as '*Estigmene Lactinea*,' is '*Eucharia mariamne*.'

Dysschema minor Becker, sp. n.

Fig. 14

Diagnosis. The smaller species in the *D. thetis* species-group, resembling *D. zeladon* (Dyar), but easily distinguished by the semitranslucent hind wings, orange in *D. zeladon*.

Description. Male forewing 26–28 mm. Head—including labial palpi and antennae—and thorax dark gray; tegulae with a broad yellow band frontally. Wings semitranslucent, veins dark gray. Forewings with basal half smoky gray; costa gray, interrupted smoky at middle and before apex; irregular, subreniform patch at end of cell; termen broadly gray; dorsum, below cell, gray, not reaching tornus; tinged ochreous underside. Hind wings with costa, above cell, ochreous; margins orange; external margin bordered black internally, with series of white dots between veins; internal margin intermixed with long, dark gray scales. Abdomen carmine red dorsally; with dorsal and two lateral black bands; underside yellow.

Genitalia male (Fig. 14). Socii long, slender, slightly incurved, tapering to sharp end. Vinculum a narrow, round belt. Juxta diamond shaped. Valvae twice as long as broad; distal half split between dorsal margin and sacculus, ending in two long, slender digital expansions, tapering distad; that of dorsal margin more sclerotized and sharply pointed than that of sacculus. Aedoeagus a nearly straight rod, three times as long as thick; vesica smooth with a single long spine.

Female unknown.

Material studied (2 ♂♂, 1 genitalia slide). Holotype ♂, MEXICO: Col, Minatitlán, 2100 m, 14.vi.2000 (Becker) (VOB 121944) (UNAM); paratype ♂, same data as holotype (VOB).

Etymology. From the Latin 'minor' = little.

Dysschema perplexum (Schaus)

Pericopsis perplexa Schaus, 1910: 210. Holotype ♂, COSTA RICA: [Limon], Sixaola Riv., iii.[1909] (Schaus & Barnes) (USNM, no. 16912) [examined].

Pericopsis guapa Schaus, 1910: 210. Holotype ♀, COSTA RICA: [Limon], Guapiles, i.1909 (Schaus & Barnes) (USNM, no. 16910) [examined]. **Syn. n.**

Remarks. A highly dimorphic species. Males semitranslucent white with transverse fasciae and veins heavily marked dark gray, similar to the males *D. jansonis*. Females with forewings black crossed by two transverse oblique white bands and with hind wings orange, resembling *Chetone* species, but readily distinguished from these by the dorsal, dark band along the abdomen. The association of male and female was possible through the material reared from eggs and larvae by A. Aiello (pers. inform.), in Panama, and by D. Janzen (pers. inform.), in Costa Rica.

Dysschema pictum (Guérin-Ménéville)

Callimorpha picta Guérin-Ménéville, [1844]: 517. Holotype ♀, BRAZIL: SP, Santos [not examined].

Pericopsis capella Druce, 1899: 233. Holotype ♀, BRAZIL: Ba

[hia]? (illegible) (BMNH) [image examined]. Synonymized by Hering, 1925: 444.

Pericopsis indecisa Walker, 1854: 347. Holotype ♀, [BRAZIL: RJ], Rio [de Janeiro] (BMNH) [image examined]. **Syn. rev.**

Pericopsis lucifer Butler, 1873: 126. Holotype ♂, [BRAZIL]: ES "Espírito Santo" [no further data] (UMO) [image examined]. **Syn. rev.**

Remarks. The caterpillars of this species were reared on the leaves of *Mikania hirsutissima* and *Senecio brasiliensis* by Spitz (1931) and by Monte (1934), and on *Vernonia polyanthes* (Asteraceae) by Travassos Filho (1947: 483–537, pls. 1–17, figs. 1–65, a–f). The last author gives a detailed description, including colour illustrations of the different forms of the adult females, correctly identifying the males as *P. lucifer* and the females, which show high chromatic variation, as *P. picta* and *P. indecisa*, following the figures in Hering (1935: pl. 63g, 64c). Apparently Watson & Goodger (1986) overlooked this work and listed all the names as valid.

Dysschema subapicalis (Walker)

Pericopsis subapicalis Walker, 1854: 352. Holotype ♀, BRAZIL: [RJ], Rio de Janeiro] (BMNH) [examined].

Pericopsis pagasa Dognin, 1919: 5. Holotype ♂, BRAZIL: SP, São Paulo (USNM) [examined]. **Syn. n.**

Remarks. This dimorphic species is restricted to the Atlantic forests of Southeastern Brazil. Before the date of Walker's publications, all collections from this region were made around Rio de Janeiro. *P. pagasa* is the fifth junior synonym.

Dysschema thetis (Klug)

Euprepia thetis Klug, 1836: 6. Lectotype ♂, MEXICO: [No further data] (Deffe) (MNHU), here designated [image examined].

Daritis thetis var. *howardi* Edwards, 1887: 165. USA: NM [not examined]. **Syn. n.**

Remarks. This and *D. mariamne* have been regarded as synonyms [see *D. mariamne* above], however the lectotype of *thetis* belongs to the same population currently known as *D. howardi*.

Dysschema thyridinum (Butler)

Pericopsis thyridina Butler, 1871: 289. Holotype ♂, ECUADOR: [No further data] (UMO) [image examined].

Pericopsis damon Druce, 1910: 171. Holotype ♀, PERU: Chanchamayo, 1000–1500 m (Watkins) (BMNH) [image examined]. **Syn. n.**

Pericopsis grassator Hering, 1925: 444. Holotype ♂, [PERU: AM], Puerto Santa Rosa [de Huayabamba], 1894 (Garleppi) (MNHU) [image examined]. **Syn. n.**

Pericopsis mosera Druce, 1907: 301. Holotype ♂, PERU: Rio Colorado, vii.viii.1903 (Watkins & Tomlinson) (BMNH) [image examined]. **Syn. n.**

Pericopsis sylvia Druce, 1910: 172. Holotype ♀, PERU: Chanchamayo, 1000-1500 m (*Watkins*) (BMNH) [image examined]. **Syn. n.**

Pericopsis talboti Dognin, 1922: 5. Lectotype ♂, COLOMBIA: San Antonio, 1800 m (*Fassl*) (USNM), here designated [examined]. **Syn. n.**

Remarks. The types of both *P. thyridina* and *P. mosera* are almost identical. *P. sylvia* had been already synonymized with *P. mosera* by Watson & Goodger, 1986: 37. In VOB there are two specimens collected in Ecuador, Napo, Misahualli, one has the ground colour translucent whitish, like in *P. thyridina*, *P. mosera*, and *P. sylvia*, the other with the same areas yellowish, as in *P. grassator*, *P. talboti* and *P. damon*, as well as a series collected in Ecuador, Tungurahua, Rio Verde which males match the type of *P. talboti* and the female the type of *P. sylvia*. *D. talboti* was described from an unspecified number of specimens from San Antonio (1800 m), Carmen (1600 m) and Tumbo, Cauca, 1000 m (*Fassl*), in Dognin's collection and others in Joyce's collection. Apart from the lectotype mentioned above, there are other four specimens in the USNM, labeled 'cotype,' and four in the BMNH, labeled 'syntype'. These are here designated paralectotypes.

Dysschema viuda (Schaus)

Pericopsis viuda Schaus, 1910: 209. Holotype ♀, COSTA RICA: Tuis, ix.1907 (*Schaus*) (USNM, no. 16911) [examined].

Centronia joiceyi Dognin, 1923: 10. Holotype ♀, COLOMBIA: Bogota, 1919 (*Apollinaire-Marie*) (USNM, no. 30544) [examined]. **Syn. n.**

Remarks. This species ranges from Costa Rica to Ecuador. In the author's collection and in the Carnegie Museum there are large series from Costa Rica and Ecuador respectively, representing both sexes, collected at elevations from 500 to 2800m. Hering (1925: 442, pl. 63g) synonymized *Pericopsis talboti* Dognin, 1922, under *P. joiceyi*. They are different species, as correctly regarded by Watson & Goodger (1986: 37, 38). The illustrations given by Hering as *P. joiceyi* represent *D. talboti*.

Hypocrita celina (Boisduval)

Calepidos celina Boisduval, 1870: 89. Holotype ♀, GUATEMALA [no further data] (BMNH) [not examined].

Eucyane escuintla Schaus, 1920: 128. Holotype ♂, GUATEMALA: Escuintla, v. (*Schaus & Barnes*) (USNM, no. 22450) [examined]. **Syn. n.**

Remarks. The type specimen of *E. escuintla* matches exactly the figure of the type of *C. celina* in Watson & Goodger (1986, pl. 1, fig. 13). These authors also synonymized *E. pylotoides* Hering, 1925, with this.

Josiomorpha cathetozosta Becker, sp. n.

Fig. 19

Diagnosis. Same size and colour as *J. penetrata* and *triangulifera*, the other two species in the genus; easily distinguished by the elongate, yellow patch before apex, perpendicular to costa.

Description. Male forewing 22 mm. Head –including palpi and antennae– and thorax black; frons with mixed white scales. Base of tegulae with two small, white dots. Coxae yellow ventrally, tibiae and tarsi black, lined white. Forewings black; broad, yellow fascia from base of costa, across cell, following Cu₂ half way, slightly incurved distally; elongate, transverse yellow patch before apex, from below costa to before mid termen. Hind wings yellow; broad black margin from apex to M₃, expanding inwards towards anal margin. Abdomen black, yellow laterally.

Genitalia ♂. Uncus triangular, tip bent ventrad in right angle, sharp distally. Saccus as long as valvae, tapering distad to a sharp end. Juxta rectangular. Membrane between aedoeagus and anus scobinate. Valva straight, twice as long as broad, tapering distad; covered with sparse setae ventrally.

Female unknown.

Material examined (2 ♂♂, 1 ♂ genitalia). Holotype ♂, GUATEMALA: Quetzaltenango, Aguas Georginas, 2500 m, 12.vii.2000 (*Becker*) (VOB, 122897). Paratype ♂, same data as holotype, genitalia slide VOB 1775 (VOB)

Etymology. From the Greek 'cathetos' = perpendicular + 'zoster' = belt.

Josiomorpha triangulifera Hering, sp. rev.

Josiomorpha triangulifera Hering, 1925: 432. Holotype ♀, PANAMA: Chiriqui (MNHU) [not examined].

Remarks. This and *J. penetrata* (Walker) are very similar, however, the last has the fascia along forewings broader and the abdomen wholly white below, whereas in *J. triangulifera* the abdomen is white but, as pointed by Hering (1925: 432), "... on each segment the white colour narrows towards the front, so that a row of white triangles is produced." Also, both are allopatric. All specimens examined were collected in Costa Rica and Panama, whereas the long series of *J. penetrata* came from Southern Mexico and Guatemala. Genitalia are also slightly distinct. Both were synonymized by Watson & Goodger (1986: 37).

Josiomorphoides gigantea (Druce)

Fig. 21

Josia gigantea Druce, 1897: 406. Holotype ♀, PANAMA: Volcan de Chiriqui (*Troetsch*) (MNHU) [not examined].

Josiomorpha flammata Dognin, 1909: 223. Lectotype ♂, COLOMBIA: Villa Elvira, 1.vii.1908 (*Fassl*) (USNM, no. 30548), genitalia slide USNM 93110, here designated [examined]. Synonymized by Hering, 1925: 434.

Remarks. This species is very similar to the following, differing by the yellow, dorsal band along the abdomen and in the shape of genitalia [see below]. A female from Costa Rica, in USNM, matches the figure

in Druce (1897: pl. 78, fig. 25), and a male in VOB, also from Costa Rica, matches the type of *J. flammata*.

Josiomorphoides dognini Hering

Fig. 20

Josiomorpha flammata "male var., cotype" Dognin, 1909: 223.

Josiomorphoides dognini Hering, 1925: 434. Holotype ♂, COLOMBIA: Cali (USNM), genitalia slide USNM 93111 [examined].

Josiomorphoides sp. ? *gigantea*; Watson & Goodge, 1986: pl. 4, fig. 65.

Remarks. Dognin (1909: 223) described *J. flammata* [= *gigantea*, above] based on three specimens, a pair whose abdomen have a yellow band along dorsum, from Colombia, Villa Elvira, and a male, with its abdomen black dorsally, from Colombia, Cali, which he called "*J. flammata*, male var. cotype." This specimen was named *J. dognini* by Hering (1925: 434). The male genitalia of the types of both forms, illustrated here for the first time, are slightly distinct, especially in the shape of valvae.

Phaloe Guérin-Ménéville

Phaloe Guérin-Ménéville, [1838]: 283. Type-species: *Pericopis cruenta* Hübner, 1823: 24, by monotypy.

Sphaeromachia Grote, 1867: 304. Type-species: *Pericopis cubana* Herrich-Schäffer, 1866: 131, by monotypy. **Syn. rev.**

Remarks. *Sphaeromachia* was treated as a subgenus of *Phaloe* by Hering (1925: 447) and reinstated as genus by Watson & Goodger (1986: 35). The similarity of male genitalia and the presence of red marks between veins at the base of fore wing costa of the type-species of both generic names indicate that they are congeneric.

Phaloe cubana (Herrich-Schäffer), **comb. rev.**

Pericopis cubana Herrich-Schäffer, 1866: 131. Lectotype ♂, CUBA: [no further data] (Gundlach) (MNHU), here designated [image examined].

Phaloe gaumeri Druce, 1884: 107. Lectotype ♂, MEXICO: Yuc, Valladolid (*Gaumer*) (BMNH), here designated [examined]. **Syn. n.**

Remarks. In VOB there is a series of specimens from Mexico: Campeche, Escárcega -one of them compared with the type series of *gaumeri*- and from Cuba. Their characters, including genitalia, are identical. There is a male and a female syntypes of *P. cubana* in the MNHU bearing identical labels: red, rectangular 'Type'; violet, square 'Origin'; white, rectangular 'Coll. H.-Sch.'; white, rectangular 'Coll. Staudinger'; white, rectangular 'Cubana H.S.,

=Gaumeri Druce.' The male specimen is here designated as lectotype, the female as paralectotype. There are two males and one female syntypes of *gaumeri* in the BMNH, all bearing labels as above, the male bearing a round red 'type' label is here designated lectotype, the others paralectotypes. The sexes are dimorphic, as illustrated in Hering (1925: pl. 64f) and in Watson & Goodger (1986: pl. 2, figs. 34, 35).

Phaloesia saucia Walker

Phaloesia saucia Walker, 1854: 359. Holotype ♀, GUATEMALA [no further data] (BMNH) [not examined]

Phaloesia fulvicollis Butler, 1876: 171. Holotype ♀, [COLOMBIA]: Sta. Marta (BMNH) [not examined]. **Syn. rev.**

Phaloesia flaviventris Reich, 1938: 207. Type(s) ♂, VENEZUELA. [not examined]. **Syn. n.**

Remarks. *P. fulvicollis* had already been synonymized with *P. saucia* by Kirby (1892), followed by Hering (1925: 448, pl. 65a). It is wrongly listed as a synonym of *Gnophaela aequinoctialis* Walker, 1854 in Watson & Goodger (1986: 34), due to a misplacement in the file card at the BMNH (D. Goodger, pers. inform.). The type material of *P. flaviventris* was examined by A. Watson, and in the BMNH there is a note by him stating "absence of white spot in forewing cell, form of *saucia*" (D. Goodger, pers. inform.). In the series examined there are specimens with the white spot on forewing cell reduced or absent, as illustrated in Watson & Goodger (1986: pl. 2, fig. 26), as well as with abdomen either yellow or black ventrally.

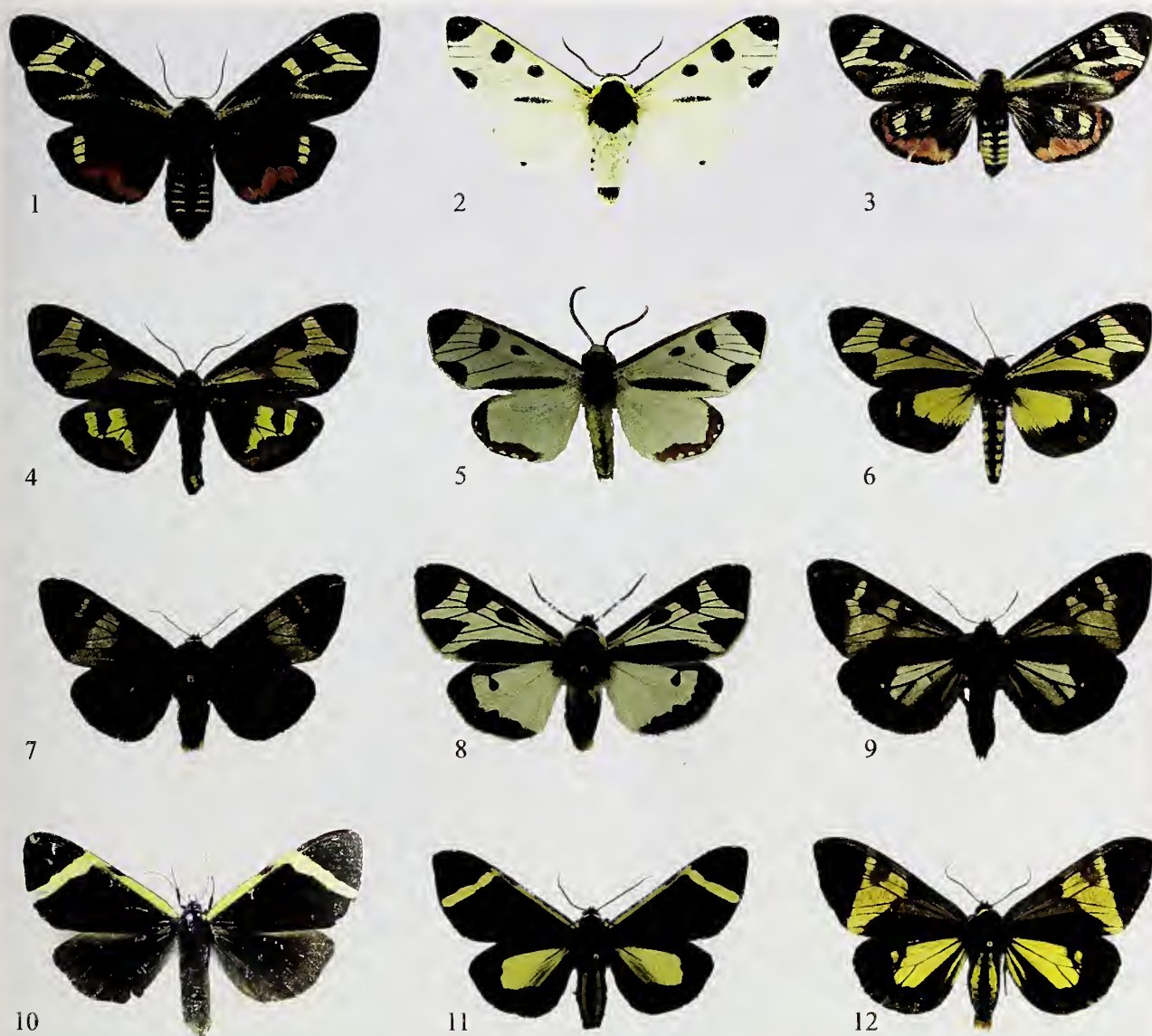
Pseudophaloe ninonia (Druce)

Eucyane ninonia Druce, 1884: 104, pl. 10, fig. 13. Holotype ♀, PANAMA: Volcan de Chiriqui (Mus. Staudinger) (MNHU) [not examined].

Pericopis cotta Druce, 1897: 385. Holotype ♂, PANAMA: Chiriqui (*Troetsch*) (Mus. Staudinger) (MNHU) [not examined]. **Syn. n.**

Phaloe levisi Schaus, 1910: 210. Lectotype ♂, COSTA RICA: [Cartago], Juan Viñas, vi. 1909 (*Schaus*) (USNM, no. 16913), here designated [examined]. **Syn. n.**

Remarks. The illustrations of both types described by Druce allow recognition of the species. The ground colour of this species can be either whitish or yellow. Specimens of the two forms collected in Costa Rica by the author, at the same place and at the same time, have identical genitalia. The type of *P. ninonia* belongs to the white form, whereas the types of *P. cotta* and *P. levisi* belong to the yellow form. There is a specimen, from Costa Rica, El Sitio, v. 1909, labeled by Schaus as "*Phaloe levisi* type female", which is here designated as paralectotype.



Figures 1-12: Adults of *Dysschema* and *Sermyla*. 1-3 *D. boisduvalii*: (1) female, (2) male, (3) female f. *rubripicta*; 4, 8 *D. innominatum*: (4) female paratype, (8) male holotype; 5, 6 *D. centenarium*: (5) male, (6) female; 7, 9 *D. luctuosum*: (7) male f. *typica*, (9) male with ground colour of hind wings white; 10, 11 *S. transversa*: (10) female holotype of *morta*, (11) male; (12) *D. fantasma*.

***Pseudophaloe promiscua* Becker & Espinosa, sp. n.**
Fig. 18

Diagnosis. It resembles *P. helotes* but easily distinguished by the iridescent blue tint on hind wings and absence of red at the tip of abdomen.

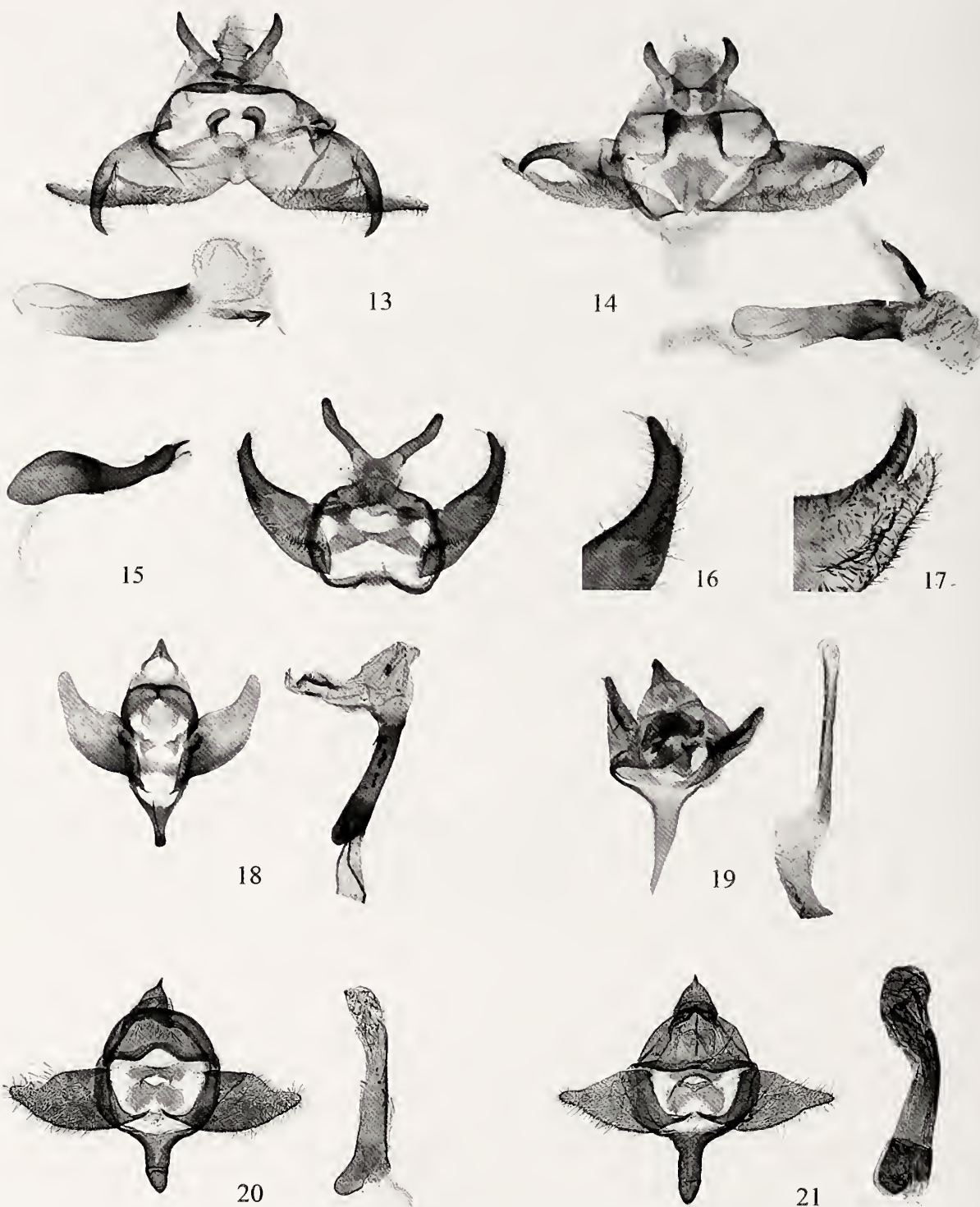
Description. Male forewings 23 mm. Head—including labial palpi and antennae—black; labial palpi with white line ventrally; frons with four white dots: two laterally and one under each scape. Thorax black; pair of white dots anteriorly and trace of white line along dorsum; patagia with pair of red dots each; tegulae with small white dot anteriorly. Legs black, lined white ventrally. Forewings opaque black; small red dot at base of costa; median, oblique, yellow fascia from below costa, across cell, to

before tornus; trace of narrow fascia before apex. Hind wings black with iridescent blue reflex. Abdomen black, tinged blue dorsally, whitish ventrally.

Genitalia ♂. Uncus a short triangle, tapering distad to a sharp tip. Saccus half as long as valva. Juxta a narrow, transverse band. Valvae twice as long as broad, distal half tapering towards round tip. Aedoeagus a straight rod, four times as long as thick; vesica smooth.

Females unknown.

Material studied (10 ♂♂, 1 ♂ genitalia slide). Holotype ♂, COSTA RICA: Limón, Res. Biol. Hitoy Cerere, 9°67'73"N-83°06'13"W, 600 m, 15.v.1999 (Barton) (INBio). Paratypes: 6 ♂♂, same locality as holotype, 200-770 m, i.ix.1990, 1.vii.1991, 15.v.1999, 12.vi.1999, 2.vii.2003, (Barton, Carballo & Barrelier); 2 ♂♂, Limón, Bribri Suretka, 9 km W Bribri, 9°62'29"N-82°77'29W,



Figures 13-22: Pericopina male genitalia, ventral view; aedoeagus removed, lateral view. (13) *Dysschema intermedium*, paratype; (14) *D. minor*, paratype; (15) *D. innominatum*, paratype; (16) *idem*, detail of left valva; (17) *D. centenarium*, detail of left valva; (18) *Pseudophaloe promiscua*, paratype; (19) *Josiomorpha cathetozosta*, paratype; (20) *Josiomorphoides dognini*, holotype; (21) *J. gigantea*, lectotype.

9.i.1983 (Janzen & Hallwachs) (INBio); ♂, Limón, Siquirres, 200 m, 27.i.1973, mating with a female *P. cerealia* (Becker) (VOB, 3925).

Etymology. From the Latin 'promiscuus' = mixed (see Remarks).

Remarks. A male (VOB 3925), was collected by the author at light, mating with a female of *P. cerealia* (Druce) (VOB 3926).

Pseudophaloe schausi (Edwards)

Pericopsis schausi Edwards, iii.1884: 59. Lectotype ♂, MEXICO: Ver, Jalapa (*Schaus*) (USNM), here designated [examined].

Phaloe verania Druce, x.1884: 107, pl. 11, fig. 7. Holotype ♂, GUATEMALA: Zapote [no further data] (*Champion*) (BMNH) [not examined]. **Syn. n.**

Pseudophaloe veranioides Hering, 1925: 430. Syntypes, ♂, ♀, MEXICO: [Sin]: Misantla, 11.vi [no further data] (MNHU) [not examined]. **Syn. n.**

Remarks. Druce (1884: 108) listed *P. schausi* just after the description of *P. verania* and stated that he had not seen the specimens, and that from the description he believed that it was very similar to *P. verania*. He was right. They are the same species. The type of *P. schausi* matches perfectly the figure of a syntype of *P. verania* in Watson & Goodger (1986: pl. 2, fig. 30), and that of *P. veranioides* in Hering (1925: pl. 60d). The specimens from Central and the West coast of Mexico are slightly smaller [f. *veranioides*] than typical specimens, and have the yellow areas much reduced and the red on abdomen restricted to the last two segments, otherwise identical. In the USNM there is a male, which matches this form, labeled "*schausi* Edw., *verania* Dr." in Schaus' handwriting. There is another male, with identical label as the lectotype of *P. verania*, here designated as paralectotype.

Sermyla transversa Walker

Figs. 10, 11

Sermyla transversa Walker, 1854: 461. Holotype ♂, [BRAZIL: RJ]: Rio [de Janeiro] [no further data] (BMNH) [examined].

Sermyla morta Schaus, 1892: 282. Holotype ♀, BRAZIL: [RJ], Petropolis (*Schaus*) (USNM, no. 11422) [examined]. **Syn. n.**

Remarks. The description of *S. morta* was based on a melanic female with its hind wings and abdomen wholly black. In the collection of UFPR there is one melanic male, collected together with a series of the normal form from Campos do Jordão, São Paulo State.

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Notes on the morphology and larval development of *Methona themisto* (Hübner, 1818) (Lepidoptera: Nymphalidae: Ithomiini) from southeastern Brazil

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Abstract. Little has been published on the natural history, immature stages and development of the Neotropical butterfly genus *Methona* Doubleday, 1847. In spite of being relatively common where it occurs, many aspects of the morphology and development of *Methona themisto* (Hübner, 1818) still are poorly known. Here we describe the morphology and duration of the egg, larval and pupal stages of *Methona themisto* in Southeastern Brazil. A single plant of *Brunfelsia uniflora* (Solanaceae) was chosen by the butterflies to lay their eggs, and larvae and pupae were reared on it. Adults were observed laying single, white eggs mostly on the abaxial surface of fresh leaves. All larval instars were black with 12 yellow bands, except for the first few days after molting, when they were dark brown with green heads and anal plates. The pupa was pendant, with a mean length of 2.24 cm. It was pale yellow with black stripes and the body was slightly bent where the abdomen joined the wing-pad apices. Mean duration of the pupal stage was approximately 14 d. We did not observe any relationship between pupal duration and weather conditions or the time of year.

Key words: *Methona*, larvae, pupa, butterfly, Nymphalidae, Ithomiini, *Brunfelsia uniflora*, Solanaceae

INTRODUCTION

The Neotropical genus *Methona* Doubleday, 1847 comprises seven species of medium-sized (wingspan about 8 cm), colorful nymphalid butterflies distributed from Costa Rica in southern Central America throughout most of South America, reaching their southernmost limit in southern Brazil, Argentina and Uruguay (Mielke & Brown, 1979; Hill & Tipan, 2008). Despite often being common where they occur, some *Methona* species are relatively poorly known. Available information on larval development of the genus is based mainly on studies of *M. confusa* Butler, 1873, *M. curvifascia* Weyer, 1883, and *M. themisto* (Hübner, 1818) (Brown, 1987; Drummond, 1976; 1986; Drummond & Brown,

1987; Willmott & Freitas, 2006; Hill & Tipan, 2008). *Methona themisto* is a relatively common butterfly, occurring in subtropical latitudes of South America and inhabiting forest edges, open areas and gardens in urban regions. The species is known mainly due to the habits of its larvae, which eat exclusively the leaves of species of the genus *Brunfelsia* (Pohl), a very common ornamental representative of Solanaceae locally known as 'Manacá' (Biezanko, 1960; Drummond, 1976; 1986; Brown, 1987; Drummond & Brown, 1987; Brown, 1992). Thus, larvae of *M. themisto* are considered pests because they may cause much damage and even total defoliation of single plants (Figueiredo-Junior, 1939; Silva *et al.*, 1968; Ruszczyk & Nascimento, 1999).

The life cycle of the species has been studied by Berg (1886), Lordello (1951), Brown & Freitas (1994) and Willmott & Freitas (2006). However, its immature stages and larval development still are poorly documented and none of these works presents a detailed morphological description of the eggs, larvae and pupae, neither makes comparisons between *M. themisto* and the other species of the genus. Here we describe details of egg morphology, and morphology and duration of the larval instars and the pupa of *Methona themisto* in southeastern Brazil, and provide notes on its natural history.

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MATERIALS AND METHODS

We made all observations from July 2012 to April 2013, in the municipality of São Paulo (23°30'32"S, 46°29'57"W), southeastern Brazil. During the first phase, between July and September 2012, we studied the 5th instar and pupa of *M. themisto* found on a single plant of *Brunfelsia uniflora* (Pohl) (Solanaceae) located in an urban garden, to record morphological aspects and natural duration of these stages. The larvae were observed directly on the plant, until they matured and ceased feeding, and wandered off in search of pupation sites. At this time they were transferred to a plastic observation box protected from potentially damaging rain and wind, where plant branches and leaves previously cut off were included. In the second phase, from November 2012 to April 2013, we observed the plant carefully for signs of oviposition, noted the morphology and duration of the egg stage and the 1st, 2nd and 5th instars, and as well made observations of larvae that we transferred to and reared in plastic boxes. These boxes were maintained under the same conditions and were cleaned and had leaves replaced daily. Observations were recorded daily and head capsules and exuviae were collected. Over the whole study, we examined, photographed or videotaped five oviposition events, 12 eggs, four 1st instars, two 2nd instars, 61 5th instar and 61 pupae. All measurements are given as mean \pm 1 SD. To record images we used a Sony HX9 Digital Camera and a GoPro Hero 2 Video Camera (all videos and photos are available from the authors on request).

RESULTS

Brunfelsia uniflora (Pohl) (Solanaceae), known locally as 'Manacá', was used as host plant by the larvae of *M. themisto*. All eggs and larvae were found on a single plant individual.

Oviposition. Oviposition ($n=5$, Fig. 6C) was observed between 11am and 1pm on sunny days, when the adult was most active and flying around the host plant. During oviposition, the female perched on the leaf, curved her abdomen below the leaf and laid the eggs mainly on the opposite side of the leaf. On a few occasions we observed the female ovipositing on the same leaf surface as where it was perched, i.e., the upper, adaxial surface. The process of oviposition lasted no more than six seconds from perching, laying and departing for another leaf. The female laid a single egg on each leaf. On a few occasions more than one egg was recorded on a single leaf.

Egg. Mean diameter 0.93 ± 0.2 mm ($n=12$), height 1.40 ± 0.10 mm (Fig. 1). The upright egg is of ovoid

shape, the chorion ornamented with parallel ribs and numerous regular dips in between. It is white and glistening, gradually darkening to buff, particularly after the 4th day. A few (2–4) days before hatching eggs became translucent, with the embryo visible inside as a dark spot (Fig. 1D).

Larva. First instar ($n=4$, length: 9 ± 2 mm). Head round, pale green just after hatching, became black at the second day. Body roughly round in cross section, dark green with 12 pale yellow thin bands on the first day, turning brown with yellow bands on the second day, and black with yellow bands from third day onwards. Anal plate pale green at the first day, became brown at the second day. Thoracic legs, prolegs and crochets pale brown at first day, became dark brown at the second day (Figs. 2A, B & C).

Second instar. As described for first instar, but black with thin yellow bands ($n=2$, Figs. 2D, E & F). Head rounded, green on the first day, becoming black the following day. Anal plate pale green on the first day, becoming brown the second day. Thoracic legs and prolegs green on first day, becoming brownish green in the second day, and black from third day onwards.

Fifth instar. Head capsule width: 4 ± 1 mm ($n=4$), body length just before pupation: 37.4 ± 0.8 mm ($n=61$). Like most of previous instars, the body was black, with thin, pale orange bands (Fig. 3). Anal plate, thoracic legs and prolegs black, crochets grey. Within a few hours before pupation, the stripes became paler (Fig. 3F). Feeding damage by all instars consisted of circular or ovoid perforations, either on the margin or in the middle of the leaf blades (Fig. 3D).

Pupa. The molt to the pupa takes place quickly, roughly 6 seconds from splitting of the larval cuticle to the process of compressing it towards the cremaster when the exuvia is discarded. Pupa (Figs. 4 & 5) pendant, slightly bent where the wing pad apices meet the abdomen, mean length 22.4 ± 3 mm ($n=8$). Fresh pupa entirely pale yellow with black cremaster (Fig. 5A). After about 30 min a few black stripes appear on the last segment before the cremaster, and after roughly 120 min black stripes and rows of black dots appear throughout the pupa (Figs. 5B & C). The pupa has two dorsal longitudinal rows of elongate spots, which are larger and more rounded closer to the cremaster. The extent of dark markings was variable among individuals, some having heavier markings than others (Figs. 5E & F for comparison). The pupa became brown roughly three days before adult eclosion, and darkened further 24 h before eclosion, with its dorsal part slightly transparent (Fig. 5G). After adult eclosion, pupal exuviae were totally translucent except for the black markings described above (Fig. 5H).

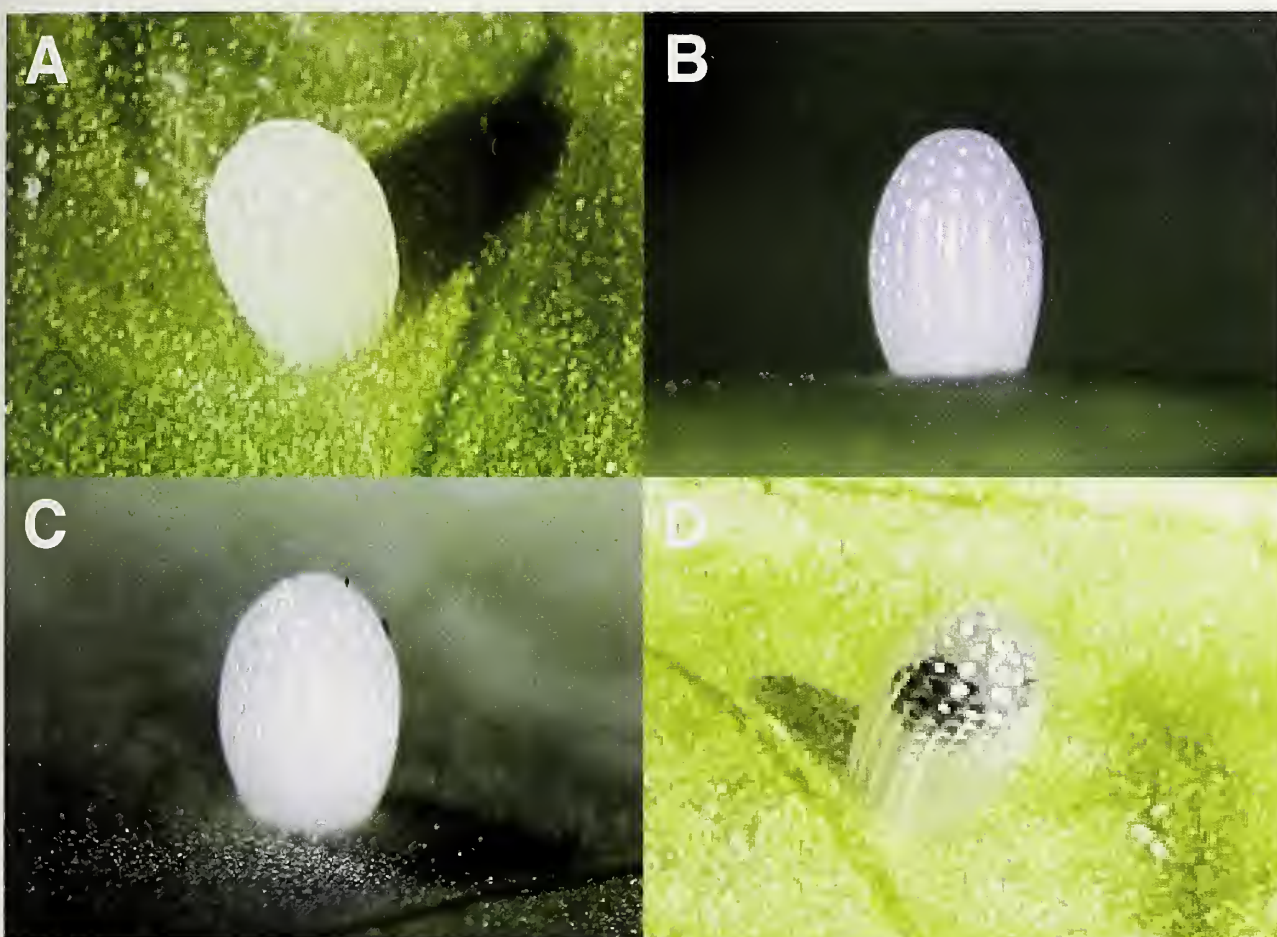


Figure 1. Eggs of *Methona themisto*. **A.** Just after oviposition. **B & C.** six days after oviposition. **D.** Shortly before hatching, blackish head capsule of larva discernible.

Mean duration of the pupal stage was 14.21 d (range: 9–23 d). Metamorphosis was not observed in 14 of the 61 individuals, but morphology was examined for all 61. Of the remaining 47 individuals, 13 (*ca* 20%) did not complete metamorphosis due to unknown reasons. In most of these cases ($n=10$), a small, hollow area (diameter 0.5 mm) appeared in the pupa, with internal liquid suspended from the inside, suggesting either predation by some arthropod, albeit no predation event was observed directly, or, more likely, that the pupa died for some reason and the internal tissue was broken down by bacteria. A single mature larva, already attached to a small twig and ready to pupate, detached and fell to the floor of its box. There it remained motionless for three days, as if dead. Surprisingly, it then transformed to a pupa, although not hanging from any branch and lying in direct contact with the sandy floor of the box.

Morphology and color of this pupa was the same as the other individuals. After 14 days as a pupa, the imago eclosed, but with seriously deformed wings. After a day of trying to walk around the container, moving its wings and trying to fly, this individual took short flights and left the box, but was unable to perform normal flight.

DISCUSSION

Although studies on Neotropical Lepidoptera have increased during the last few decades, for the majority of butterflies of the region still basic information on their life-cycles is lacking (Vane-Wright & Ackery, 1989; Moraes *et al.*, 2012). Despite being common where it occurs, this also applies to *Methona themisto*. The species is known mainly due to the habits of its larvae, which eat exclusively the leaves of *Brunfelsia uniflora* (Pohl), a very common

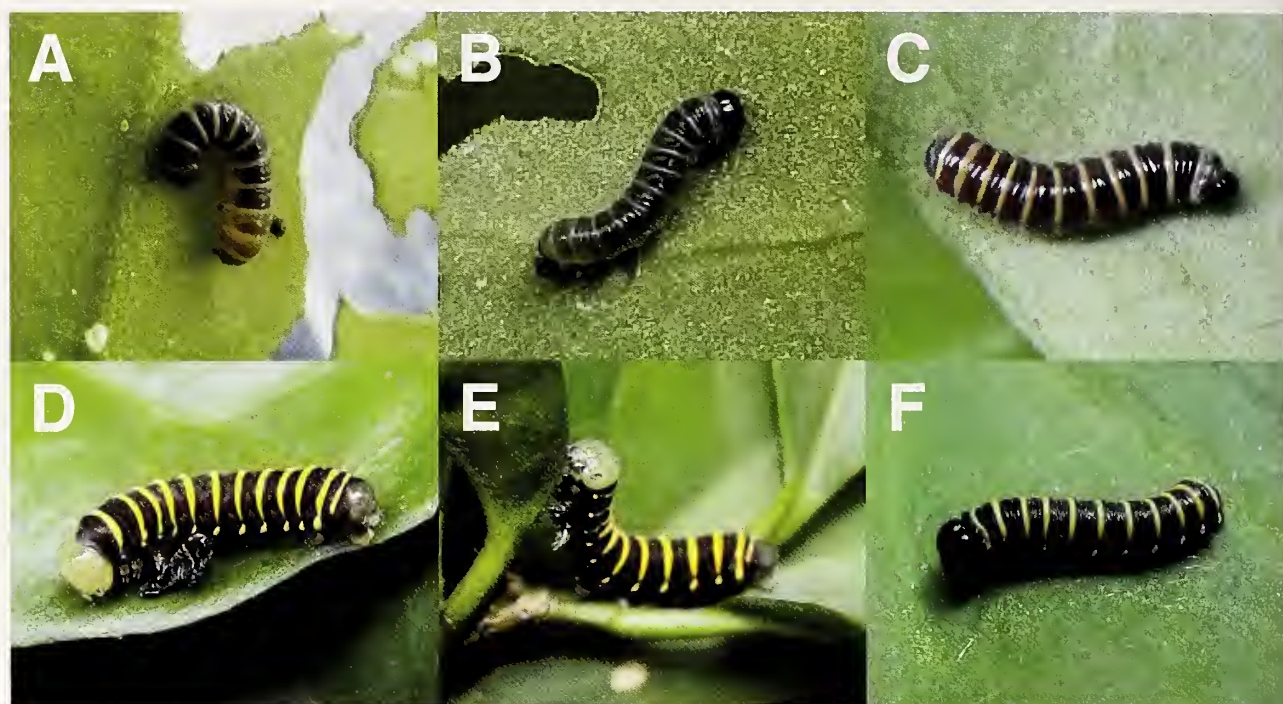


Figure 2. Larvae of *Methona themisto*. **A.** First day of first instar. **B.** Second day of first instar. **C.** Third day of first instar. **D** and **E.** First day of second instar. **F.** Second day of second instar.

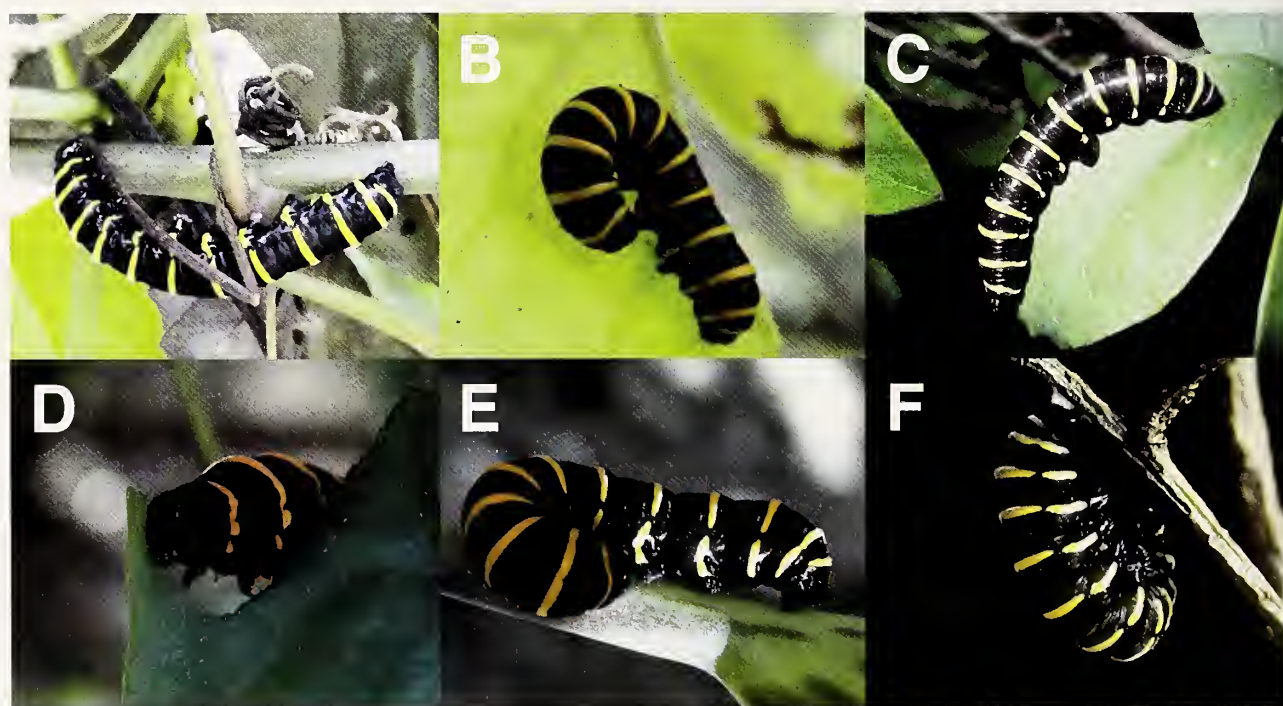


Figure 3. Fifth instar of *Methona themisto*. **D:** larva while feeding; **F:** just after fastening for pupation.

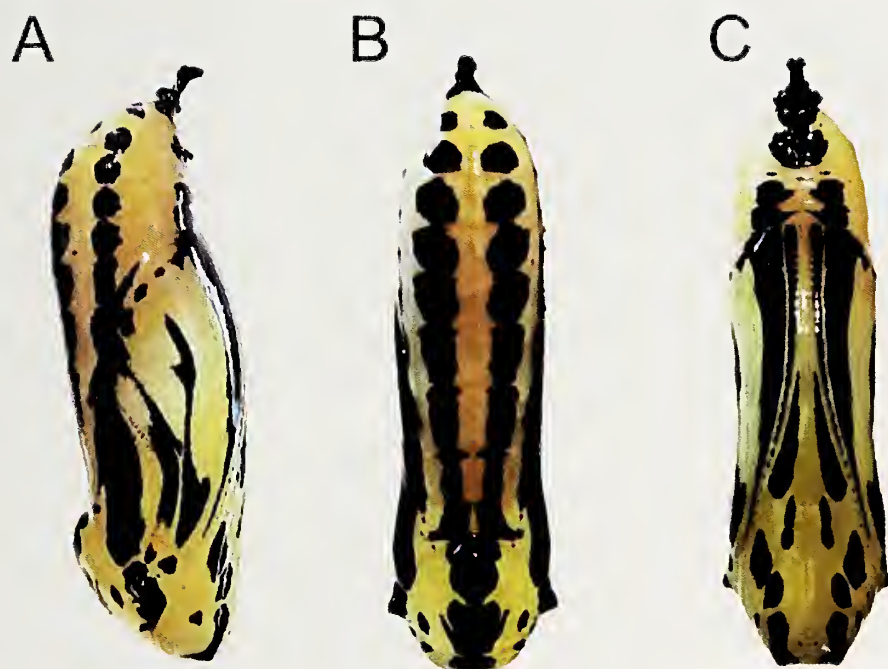


Figure 4. Pupa of *Methona themisto*. A. Lateral view. B. Dorsal view. C. Ventral view.

ornamental Solanaceae plant (Biezanko, 1960; Brown, 1992). The larvae of *M. confusa* and *M. curvifascia* are also known to feed on another species of that genus, *B. grandiflora schultesii* Plowman, and both these *Methona* species can even be found together on a single plant (Hill & Tipan, 2008).

The leaves of the larval host plant where eggs and larvae were found varied greatly in size and age. Eggs were observed mostly on the abaxial side of the leaves, even though a few eggs were recorded on the adaxial surface. Only single eggs were encountered on the host plants and observed during oviposition. We found no evidence of eggs laid in clusters by *M. themisto*. In just one case we recorded two eggs on the same leaf, however they were a few centimeters apart. Most species of Ithomiini are known to lay single eggs, although a few have been reported as cluster-laying, such as species in the genera *Mechanitis*, *Hypothyris*, *Episcada*, *Ithomia*, *Pteronymia* and *Methona* (Hill & Tipan, 2008). However, intraspecific variation in oviposition behavior has been reported for some ithomiine species, e.g., *Mechanitis menapis* and *Hypothyris euclea* are known to lay eggs in clusters in Costa Rica, but single eggs in Ecuador (Gilbert, 1969; Drummond, 1976; Hill & Tipan, 2008). Among the species of *Methona*, only *M. confusa* is known

to lay eggs in clusters in some parts of its range (Hill & Tipan, 2008), but a record of a solitary larva from Venezuela suggests that it may also lay single eggs (Brown, 1987; Hill & Tipan, 2008). It would be interesting to examine whether the single-egg pattern is consistent throughout the entire range of *M. themisto* or whether it varies according to hostplant quality, geographical region or season.

Concerning larval development, our observations provide details on the morphology of many stages in the development of *M. themisto*, mainly concerning the colors and patterns of larval head, segments, legs and prolegs, as well as on the pupae. Most instars of *M. themisto* are quite similar in morphology to those of congeneric species, such as *M. confusa* and *M. curvifascia* (Hill & Tipan, 2008). Nevertheless, the larvae of *M. themisto* are easily distinguished from those of *M. confusa* and *M. curvifascia* mainly by the color and width of the yellow bands, which are narrower and darker, tending to orange, in the former, and paler and wider in *M. confusa* and *M. curvifascia*, whose larvae are very similar to each other (see Figs. 2 and 3 in Hill & Tipan, 2008). Regarding the first instar, the color of head capsule, thoracic legs and prolegs is similar between *M.*



Figure 5. Lateral view of pupa of *Methona themisto*. **A.** Just after pupation. **B.** 30 min after pupation. **C.** 60 min after pupation. **D.** 120 min after pupation. **E.** 24 h after pupation. **F.** Three days after pupation, showing an extremely heavily marked pattern of spots and stripes. **G.** 24 h before eclosion. **H.** pupal exuvia.

themisto observed here and *M. confusa* and *M. curvifascia*. However, the color of the head and anal plate in the first day of *M. themisto* was pale green, instead black as reported in first hatched larvae of *M. confusa* and *M. curvifascia* (Hill & Tipan, 2008). Furthermore, the anal plate, thoracic legs, prolegs and crochets in the first instar of *M. themisto* were dark brown, not black as reported for the other two *Methona* species. The same was observed in the second instar, which had green head and anal plate on the first day and became black and dark brown, respectively, in the second day. The fifth instar is very similar in morphology among *M. themisto*, *M. confusa* and *M. curvifascia*. On the other hand, larvae of *M. megisto* are strikingly distinct from the remaining *Methona* species by the large width of the yellow bands in their lateral portion, just above the thoracic legs and prolegs (see Willmott & Freitas, 2006).

The larvae of *M. themisto* have 12 transverse yellow bands, including one on segment A9, which is also present in *M. megisto* and *M. confusa* (Brown, 1987; Brown & Freitas, 1994; Hill & Tipan, 2008).

This pattern is considered a synapomorphy of the genus by Willmott & Freitas (2006). However, *M. curvifascia* lacks the band on A9, presenting 11 bands in total (Hill & Tipan, 2008), indicating that this character varies within the genus. Thus, from a systematic view, either the lack of a transverse band on A9 can be a plesiomorphic condition in that species, and the evolution of an extra-band occurred after the divergence of that species from the rest of the group. Or, the presence of the band on A9 in the ancestor was followed by a secondary loss in *M. curvifascia*. A molecular study places *M. curvifascia* as the basal *Methona* species (Hill & Tipan, 2008), what may indicate that the former hypothesis is more likely, *i.e.*, the lack of an extra-band as a plesiomorphic character in *Methona*. From the same perspective, assuming *M. curvifascia* as the most basal *Methona* species, the width and color of the bands, which are extremely similar in *M. confusa* and *M. curvifascia*, are likely to be plesiomorphic in these two species.



Figure 6. Imagos of *Methona themisto*. **A.** Foraging. **B.** Copulating. **C.** Ovipositing, egg being laid on the adaxial (upper) face of the leaf. **D.** Adult just after eclosion from the pupa. **E.** Adult 2 h after eclosion.

The traits observed here in *M. themisto* are highly congruent with the following characters of *Methona* larvae listed in Willmott & Freitas (2006), with their character states indicated in parentheses: 22(1) absence of subdorsal filaments in the last instar; 49(1) presence of a conspicuous colored ring on A9; 54(0) a straight pupa; 55(1) presence of a pronounced curve on the dorsal edge of abdomen in posterior half to cremaster; 56(0) a slightly indented dorsal edge of abdomen at thorax-abdomen suture; and 59(0) smooth dorsal edge of abdomen at third abdominal segment. Nevertheless, Willmott & Freitas (2006) reported that *M. megisto* and *M. themisto* lay eggs preferentially at the border of leaves, listing this as a synapomorphy for the genus (p. 26, character 9:1). Even though we observed eggs being laid by *M. themisto* in the border of some leaves, oviposition location did not seem confined to leaf edges, but instead it appeared to occur at random on the leaf surface. In the same way, *M. curvifascia* does not seem to lay eggs preferentially near the leaf border, and *M. confusa* lays eggs in clusters covering a large portion of the leaf (Hill & Tipan, 2008). Thus, the existence of different patterns of oviposition and their systematic importance must be re-evaluated within the genus *Methona*.

Extensive intraspecific variation was observed in the shade and extent of the black markings on the pupae of *M. themisto*. The extent of the black markings in this species appears to be more similar to *M. confusa* than to *M. curvifascia*, which has smaller black stripes and spots (Hill & Tipan, 2008). The range of variation in the black markings in the pupae of *M. themisto* was comparable to, or even larger than reported for *M. confusa*. It needs to be evaluated if the shape and extent of these markings can be useful for taxonomic studies. Duration of the pupal stage varied from 9 to 23 d, with a mean of 14.21 d, comparable to that reported for *M. confusa* and *M. curvifascia*, in which the length of the pupal stage varies from 11 to 12 days (Hill & Tipan, 2008).

The data presented here, especially concerning the morphology and other detailed aspects of the larval development of *M. themisto*, contribute to fill some gaps on the knowledge of the genus *Methona*. The intraspecific variation in many aspects of the species' development could be a fruitful area for investigation, and this study underscores the importance of continuing research that focuses on the immature stages in *Methona*, as well as other ithomiine species, in order to better understand their biology, systematics, and conservation.

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NOTE

Honeydew feeding in adult Noctuidae and Erebidae – some observations and a note on differing modes of access

Honeydew is the sugary excrement of various phloem sap feeding insects, particularly hemipterans, which is a major sugar source for many invertebrates (Stadler & Dixon, 2005; Wäckers, 2005). The attractiveness of honeydew to moths is long known (e.g. Wilkes, 1748-49). Nevertheless, published reports are sporadic (Pittioni, 1923; Johnson & Stafford, 1985; Leverton, 2001) and there is uncertainty over whether honeydew constitutes an important food source for adult Lepidoptera. Allan (1937) reckoned it to be the principal food of many species in the adult stage while more recently Johnson & Stafford (1985) concluded that they (excepting the Lycaenidae) probably 'rarely consumed' honeydew. Stoffolano (1995) considered the possibility that honeydew could be 'a major carbohydrate food source for adult lepidopterans' plausible but called on the need for evidence. Since then very considerable advances in understanding of mouthpart morphology, function and evolution in the Lepidoptera have been made and their relationship to feeding guilds elucidated (Petr & Stewart, 2004; Krenn, 2010; Zaspel *et al.*, 2011; Zenker *et al.*, 2011). For moths the focus of such work has fallen on fruit feeding, fruit piercing, skin piercing and lachryphagous genera – groups which hold a particular human interest or economic importance. Information on the adult feeding behaviour of many groups of nocturnal moths in general – and specifically about the use of honeydew – remains vague. Their honeydew feeding niche whilst perhaps not of economic importance is of significant ecological interest.

In published observations of moths found at honeydew in the British Isles which include details on the manner of feeding (many do not) most apparently

relate to honeydew which has fallen onto surfaces – typically upper leaf surfaces – beneath leaves or stems supporting aphids and is in a liquid state (e.g. Meldola, 1869; Leverton, 2001). I have been unable to find any reference to moths feeding at dried honeydew or interacting while foraging for honeydew with ants attending the producing aphid colony. References to the ingestion of honeydew by a moth directly from a producing aphid are rare (Esche, 1994; Steiner, 1994). The purpose of this note is to document instances of these behaviours and to put on record some observations which illustrate three distinct modes of moths (Lepidoptera: Noctuidae and Erebidae) winning access to the carbohydrate resource provided by aphids. All observations reported here were made in Hargate Forest in the High Weald 'Area of Outstanding Natural Beauty', UK (51°6' N, 0°14' E) in summer 2009. A secondary purpose of this note is to contribute to the documentation of those species of moth which feed on honeydew. As Corke (1999) remarks, even for the relatively species-poor and intensively observed British Rhopalocera fauna, data on which species use honeydew are limited; the same applies equally to macromoths.

On the night of 20th-21st June 2009 five species of noctuid were recorded feeding at honeydew on leaves of Stinging Nettle (*Urtica dioica* (Linnaeus)): *Noctua pronuba* (Linnaeus, 1758); *Diarsia mendica* (Fabricius, 1775); *Diarsia brunnea* (Denis & Schiffermüller, 1775); *Euplexia lucipara* (Linnaeus, 1758); *Apamea monoglypha* (Hufnagel, 1766). There were also individuals of *Hypena proboscidalis* Linnaeus, 1758 (Lepidoptera: Erebidae) and *Blastobasis lacticolella* Rebel 1940 (Lepidoptera: Blastobasidae) feeding. The moths were observed between 23:00 and 01:00. Large numbers of the Common Nettle Aphid (*Microlophium carnosum* Buckton, 1876), a species which is not attended by ants, were feeding from the stems of the plants. It was not a dewy evening, but many nettle leaf surfaces were coated with moist honeydew while others were only partially covered, the honeydewed areas being visible as glistening blotches. The whole of May and June had been relatively dry up to this point and there had been no significant rainfall in the preceding week during which the minimum-maximum temperature range was approximately 10°C

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to 22°C. The moths were active and alert and easily disturbed by the observer's approach. They regularly shifted their positions on the leaves or ran to other leaves, apparently 'foraging movements' to areas of greater moisture after a feeding patch became drained. During July, in eight subsequent visits to the same forest track, which had large stands of *U. dioica* along its ditches and verges, no moths were witnessed feeding at honeydew.

On the evening of 16th August between 23:00 and 00:00, at the same site, four other common noctuids were observed apparently feeding at honeydew from Rosebay Willowherb (*Chamaenerion angustifolium* (Linnaeus) Holub) leaves: *Ochropleura plecta* (Linnaeus, 1761); *Noctua janthe* (Borkhausen, 1792); *Xestia c-nigrum* (Linnaeus, 1758); *Phlogophora meticulosa* (Linnaeus, 1758). The plants in question were heavily populated by a species of *Aphis* (possibly *A. salicariae*) which formed colonies along the midribs on the leaf undersides. However, in this instance the upper leaf surfaces from which the moths fed – many of which were yellowing and curled at their margins – were all dry to the touch and without any visible moisture. The plants still had some flowers on them. These are known to be fed from by noctuid and geometrid moths (Leverson, 2001) but on this occasion no moths were observed visiting them. Both daytime and night-time temperatures had in general been higher than in June but with a similar lack of rainfall in the week or more before the observation. The temperature range in this week was approximately 14°C to 25°C.

It was possible to observe the *Phlogophora meticulosa* individual for a period of more than five minutes as it dabbed and swept a small area of surface near a leaf's midrib with the dorsal tip region of its bent proboscis. It did not move its legs and with the exception of the proboscis appeared quite motionless. The proboscis tip itself was sometimes raised momentarily but most of the time was in contact with the leaf along with the rest of the tip region. A sequence of photographs indicate that at least at one point the proboscis tip region became immersed in a small volume of liquid which had not been on the leaf surface nine seconds previously (Fig. 1). My interpretation is that this moth was discharging fluid in order to mobilise sugars dried onto the surface of the leaf before then imbibing this re-dissolved honeydew. The process whereby butterflies ingest nutrients from dry material using pulses of rapidly discharged and withdrawn saliva has been described by Downes (1973) and by Knopp and Krenn (2003). The other possibility is that the moth had accumulated minute particles of moisture from the leaf surface amongst the sensilla of its proboscis

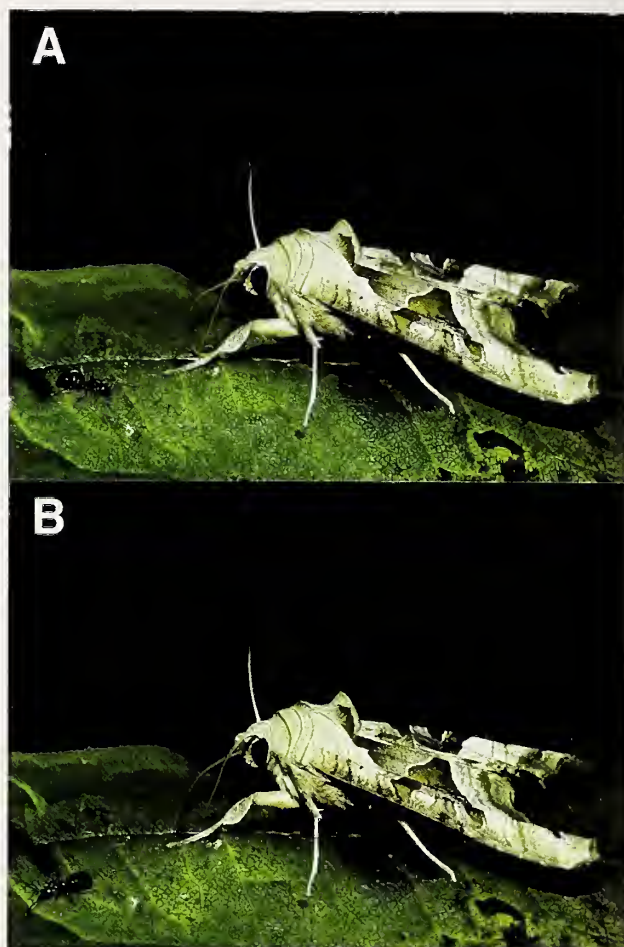


Figure 1. *Phlogophora meticulosa* adult apparently accessing dried honeydew in the presence of an ant: a) shows proboscis with tip lifted after a period when the tip region was pressed flat against the leaf and repeatedly moved about within a small area of 1 or 2 cm² of leaf surface near the midrib; b) shows a small quantity of fluid at and around the area of contact between the proboscis tip region and leaf surface, the wetted part of the yellow proboscis having become translucent.

tip region and then deposited them as a consolidated droplet, but this seems unlikely given the obvious dryness of the leaf surface and the speed with which the fluid appeared.

As the moth fed the leaf was visited by a patrolling ant (*Lasius fuliginosus* (Latreille, 1798)). On approaching within a few millimetres of the moth's front tarsi and proboscis the ant turned away leaving the leaf surface and walked to another part of the plant. *Noctua janthe* and *Xestia c-nigrum* were noted to be present on separate leaf surfaces with the dorsal tip regions of their proboscises pressed into contact with the dry leaf surface and assumed also

to be feeding. No ants were seen to investigate these moths. *Ochropleura plecta* was seen in a similar habit on the surface of a *Rubus fruticosus* (Linnaeus) leaf underneath the same aphid colony where honeydew had evidently dripped.

Another species of moth, *Xestia xanthographa* (Denis & Schiffmüller 1775), was witnessed feeding on honeydew on *C. angustifolium* simultaneously but in a different way. This species was seen to run along the vertical stem of the plant and then dart out of sight beneath leaves. The action was rapid and difficult to follow; one needed to assume a position on the ground amongst the dense stand of *C. angustifolium* looking up at the undersides of the leaves but do so without jarring the plants so much that any moths present fell or flew away. This revealed a moth to be probing amongst the aphids attached to the midrib region of the leaf. Changes in position were achieved both by running along the midrib (the moth 'upside-down') and head and proboscis movements. These movements were repeatedly punctuated momentarily for two or three seconds while the dorsal tip region of the proboscis was held either in very close proximity to, or in tactile contact with, an aphid (Fig. 2). Figure 2 shows the dorsal tip region of the proboscis pressed against an aphid's abdomen, the tip itself about level with the siphunculi. Immediately after the photograph was taken (within five seconds) an ant approached urgently along the midrib from the direction of the leaf tip. The ant made contact with the tarsus of the moth's left front leg causing the moth to recoil its proboscis and move the leg to the leaf margin, repositioning itself with its head pointing upwards and towards the upper leaf surface. It was, however, reluctant to leave the aphid aggregation and remained in this position while the ant circled it making repeated runs at the moth's tarsi which it shifted in irritation but did not move away. This continued for between 30 seconds and a minute, after which the moth ran back to the main stem and onto the top of another leaf. After a short interval of about two minutes the same moth was observed foraging in the same way on the underside of another leaf with an aphid aggregation along its midrib.

The observations recorded here display three distinct approaches used by moths to obtain food from aphid honeydew. The first, whereby fluids are freely ingested from a wet surface or sometimes from patches of liquid honeydew on an otherwise dry leaf surface, is apparently as described by other observers of moths on *U. dioica* leaves (Greene, 1863; Meldola, 1869; Colthrup, 1916; Leverton, 2001). The potential importance of this particular sugar source (honeydew deposits on *U. dioica* leaves) to adult



Figure 2 *Xestia xanthographa* adult with proboscis in tactile contact with an aphid on *Chamaenerion angustifolium* foliage apparently attempting to access honeydew direct from the producer. Shortly after the photograph was taken the moth's tarsus was attacked by an ant.

moths in the British Isles was first communicated by Greene (1880), who reported 37 species (including some geometrids and a pyralid as well as noctuids) using it. June appears to be the optimum time for this 'natural attraction' (although Greene does list a few late summer and autumn flying noctuids). In 2009 at my location conditions became wetter in late June and July, a possible explanation for the apparent cessation of honeydew feeding in July therefore being that honeydew deposits had been washed away by rain (Leverton, 2001). However, populations of *Microlophium carnosum* are known to peak in June anyway, and crash rapidly afterwards – probably owing to intraspecific competition and a deterioration in the food quality of the host plant (Perrin, 1976) – so the apparent correlation with weather conditions may be specious. The other common aphid species hosted by *U. dioica* in the British Isles, *Aphis urticae* (Gmelin, 1790), also forms dense colonies in spring and early summer, the species later aestivating as a population of small and dispersed individuals (Dixon, 1998).

The conditions stated for honeydew to be effective as a 'natural attraction' to moths in the British Isles are dewy (Collins, 1890-91; Tutt, 1902; Leverton, 2001) or foggy (Forsyth, 1890-91) evenings during dry or hot spells. In these periods of relative drought aphid populations are said to increase rapidly and the resulting excess of honeydew can accumulate on surfaces without being washed away by rainwater. Dew or damp night air on the other hand may soften or dissolve dried and crystallised honeydew deposits

(or dilute those that have become viscous through evaporation at the leaf surface) an implication being that this may render the carbohydrates more accessible to fluid feeding Lepidoptera (Merrifield, 1906; Leverton, 2001). However, since various butterflies utilise honeydew by day, including some species of the Lycaenidae for which it is the principal food source in the adult stage (Corke, 1999; Thomas, 2010), it follows that dew or other very particular meteorological conditions need not be absolutely necessary for uptake of honeydew by the lepidopteran proboscis. In the first case described here, since temperatures were not excessive in the week of the observation, the rainless conditions may have contributed to the build-up of honeydew deposits which were able to remain sufficiently moist by nightfall for Lepidoptera to easily access them.

Two months later however, in the second case, dried honeydew was apparently being used as a food source by four noctuid species. Stoffolano (1995) makes the point that while some adult lepidopterans are able to exploit nectars above optimal concentration or viscosity by using saliva to dilute them (for example *Autographa gamma* Linnaeus 1758; Proctor & Yeo, 1972) the question of whether Lepidoptera can detect, and subsequently process, dried honeydew does not seem to have been addressed. The observation here on *P. meticulousa* supports a belief that some noctuids can do so.

Although the question was raised as long ago as the 1840s (Logan, 1849), how moths detect honeydew (either in a dried or liquid state) does not seem to have been explained yet. Johnson and Stafford (1985) suggest that low apparency of both honeydew and its producers (relative to visually advertised floral nectars) may be a factor which limits lepidopteran access to honeydew. This interpretation does however seem to be founded on the visual (or partly so) foraging of diurnal Rhopalocera not on night-flying moths (which comprise the majority of lepidopteran species) which, as they do note, are evidently capable of locating sugar sources such as tree sap and artificial bait using other, presumably olfactory, stimuli. There are numerous historical, and anecdotal, examples of moths being preferentially attracted by honeydew over other, ostensibly more conspicuous, food sources, both natural and artificial (e.g. Logan, 1849; Woodforde, 1895). Norris (1936) placed honeydew into a class of foods which “can only be detected by their smell” and therefore, since the sugars themselves are not volatile, “are only attractive in a fermenting state.” However, although alcohol is perhaps a candidate, the chemical identity of any volatiles emitted from honeydew which might function as a remote (i.e. while not in tarsal contact with the honeydew) attractant to nocturnal moths does not seem to have been determined, nor

the distance range of their detectability. In other insect orders honeydew has been shown to function as a kairomone, involved in prey or host location for various predators and parasitoids of hemipterans (e.g. Wäckers, 2000). Van Emden & Hagen (1976) showed that a breakdown product of tryptophan (an amino acid present in some honeydews) was attractive to a neuropteran aphid predator. Recently Leroy *et al.* (2011) have shown bacteria in honeydew to emit volatiles to which a dipteran aphid natural enemy responded. Aphids themselves can emit volatiles including, but not limited to, alarm pheromones (Francis *et al.*, 2005). There is therefore a possibility of honeydew food sources being located indirectly by the olfactory detection of their producers. These various semiochemical systems are as yet poorly understood but there are clearly a range of possible signal types that adult Lepidoptera might read in order to find honeydew for feeding purposes.

In the third case, *Xestia xanthographa*, appears to have imbibed honeydew directly from aphids. The observation was too brief to confirm if the moth actually stimulated the aphids to release honeydew but this seems probable. The moth's initial reluctance to retreat from the aphid aggregation and its rapid adoption of another one having been challenged by the ant suggests a behaviour more purposeful than the opportunistic gleaning of sugars. All the insects involved were ‘upside-down’. Any unsolicited honeydew emissions would therefore have tended to fall away from the foraging site. Together with the fact that the aphid colony was apparently ant defended the simplest explanation for the moth's observed actions seems to be that it sought to capture the ants' honeydew harvest and that it possesses a suitable technique for doing this.

The behaviour of *Xestia xanthographa* described here may be analogous to that reported by Johnson and Stafford (1985) whereby two species (also Noctuids, *Aseptis characta* (Grote) and *Parabagrotis exsertistigma* (Morrison)) were observed feeding on aphid honeydew on *Artemisia tridentata* (Nuttall) in a canyon in Idaho, USA. These insects moved their proboscides from aphid to aphid in a way likened to ‘locating composite inflorescences and probing individual florets’ although it is not precisely clear from the report whether this was interpreted as active stimulation of honeydew secretion or just gleaning of excess honeydew from the aphids' feeding site.

Tactile stimulation of hemipterans, by the lepidopteran proboscis, to elicit honeydew excretion is known to occur but has not been widely reported. It is the main adult feeding strategy in some Asian Lycaenidae (subfamily Miletinae) (Fiedler, 1993). It

was also reported in 1928 that *Yponomeuta cognatella* (Hübner) (Yponomeutidae) in the course of 'prodding at leaves' would sometimes prod aphids with extended proboscis causing them to exude drops of honeydew (which were then consumed). However, these were captive insects and, at the time, the moths' stimulation of honeydew exudation was interpreted to be unintentional (Thorpe, cited in Norris, 1936 and Scoble, 1992). In the Atlantic forest of Costa Rica recently, a noctuid moth, *Elaeognatha argyritis* Hampson, was seen to tap the wings of a lantern bug (Fulgoridae) not with its proboscis, but with its antennae, which resulted in the ejection of a honeydew stream then caught on the moth's partially extended proboscis (Naskrecki & Nishida, 2007).

Regardless of whether the behaviour of *X. xanthographa* described here can be construed as imitation of ant-aphid attendance it does show that moths are capable of locating and obtaining honeydew directly from aphids even in the presence of attending ants. Wäckers (2005) stated that "in heavily tended colonies honeydew is often not accessible to insects other than ants." In this instance it seems that ant attendance levels were high enough to impose some foraging risk on the *Xestia xanthographa* individual but insufficient to render the honeydew inaccessible to other insects (honeydew had accumulated on some leaf surfaces underneath aphid aggregations). Presumably the compensating advantage for the moth of this behaviour was the elimination of the cost of dealing with the problems of evaporation and crystallisation to which honeydew sugars are prone (Wäckers, 2000). In this respect the behaviour presents an interesting contrast with that of the *P. meticulousa* also described in this note.

Although honeydew may be unreliable as a 'natural attraction' this may belie its importance as a food source. Allan (1937, 1945) claimed that honeydew was the principal food of many Lepidoptera in the adult state, particularly woodland moths. Johnson and Stafford (1985) considered that the "paucity of observations on this behaviour" in non-lycaenid Lepidoptera could be due to the insects being "less conspicuous when feeding on honeydew than when feeding on nectar." Moreover, even though recent reports are not plentiful there are sufficient historical references to honeydew feeding in Europe to at least demonstrate that the habit cannot be rare (e.g. South, 1878; Barrett, 1893-1907; Scorer, 1913). The diversity of species recorded at honeydew by some observers (e.g. Pittioni, 1923; Dancy & Savage, 1945; Leverton, 2001) further supports the belief that this type of feeding behaviour is not untypical in nocturnal Lepidoptera, particularly in view of honeydew's ubiquity as a sugar source in many habitats (Wäckers, 2005).

The observations detailed in this note suggest that moths are capable of utilising honeydew as a carbohydrate source in varying circumstances and using a variety of foraging techniques – and not under any especially unusual ecological or environmental conditions. This further supports the notion that honeydew feeding in adult Lepidoptera may be more commonplace than the assumption of a predominantly nectar based diet, so often attached to general accounts of the Lepidoptera (e.g. Gullan & Cranston, 2010), indicates.

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Distribution and abundance of a threatened stem-boring moth, *Houdinia flexilissima*, (Lepidoptera: Batrachedridae) in New Zealand peat bogs

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Abstract. The threatened stem-boring moth, *Houdinia flexilissima* (Lepidoptera: Batrachedridae), is known only from one host plant, *Sporadanthus ferrugineus*, which is also threatened. *Sporadanthus ferrugineus* is known from three isolated peat bogs in the Waikato region, New Zealand (Kopuatai, Torehape and Moanatuatua) and four other wetlands following translocation (Lake Komakorau, Lake Serpentine and Waiwhakareke) or restoration (Torehape peat mine). The distribution and abundance of *H. flexilissima* was assessed using a new monitoring technique which involved counting, harvesting and dissecting the *Sporadanthus* stems for the presence of larvae. The moth was found in natural, translocated and restored wetlands. *Houdinia flexilissima* appears to be able to survive wherever *S. ferrugineus* plants are present, and is most common in stems 2.0–4.5 mm in diameter. It has established in small translocated populations (≤ 270 m²) from larvae contained within stems of the original translocated *Sporadanthus* plants, and at the restoration site by dispersal from adjacent natural populations 800 metres away. From a conservation perspective, the pattern of population establishment in the absence of additional interventions is encouraging for the long-term persistence of *H. flexilissima*. Herbivory rate, larval density and larval size varied with the time since translocation, age of the restoration plantings and size of the natural wetlands. The sampling method used could be applied to ecological studies investigating other stem-boring Lepidoptera taxa.

Keywords: conservation, threatened taxa, wetland, sampling method.

INTRODUCTION

There has been a dramatic worldwide decline in the extent and health of wetlands (Keddy, 2000). Globally, peatlands are the most widespread of all wetland types, covering over four million km² (3%) of the planet's land surface, and in particular comprise a significant proportion of the boreal and subarctic regions in the northern hemisphere. In contrast, Australasian peatlands generally occupy a small proportional area, are restricted in their distribution and very few remain in their natural state (Whinam *et al.*, 2003). For example, more than 75% of the original area of restiad peat bogs (dominated

by species in the angiosperm family Restionaceae) in northern New Zealand have been converted to agricultural use. Such New Zealand restiad bogs are distinct from northern hemisphere *Sphagnum* bogs because their vegetation is characterised by two endemic restiad species: *Sporadanthus ferrugineus* and *Empodisma robustum* (Wagstaff & Clarkson, 2012), the remains of which commonly compose the bulk of peat deposits (Thompson *et al.*, 1999). Restiad bogs dominated by *Sporadanthus ferrugineus* originally covered more than 100,000 ha of northern New Zealand (de Lange *et al.*, 1999), where they formed extensive domes with peat depths up to 12 m. These bogs now represent one of New Zealand's most threatened ecosystems because of widespread drainage and conversion to pasture during the last 150 years (de Lange *et al.*, 1999). As with wetlands in general, peat bogs have multiple values, including filtering sediments, sequestering carbon, moderating the effects of floods, regulating water quality, and providing habitat for indigenous flora and fauna (Costanza *et al.*, 1997; Watts & Patrick, 2001).

There has been a paucity of entomological research associated with New Zealand peat bogs although their invertebrate fauna is known to

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be relatively depauperate and includes some specialized species (Watts & Patrick, 2001). For example, in 2003 a highly peculiar lepidopteran larva was discovered feeding in the narrow stems of *Sporadanthus ferrugineus*, at Torehape bog, and was identified as a new genus and species of moth (*Houdinia flexilissima*: Batrachedridae; Hoare *et al.*, 2006). The only known host is *S. ferrugineus*, an endemic dioecious perennial restiad with smooth wiry culms (stems) up to 3 m high that form dense swards (de Lange *et al.*, 1999). However, the extent of peatland loss resulted in *S. ferrugineus* being listed as a threatened species that occurs naturally in only three Waikato wetlands (Kopuatai, Torehape and Moanatuatua; Fig. 1). Larval damage present on historical herbarium specimens (Allan Herbarium, Landcare Research; Waikato University) suggests that *H. flexilissima* was formerly distributed throughout the Waikato, wherever *S. ferrugineus* occurred (Hoare *et al.*, 2006). To increase the number of populations *S. ferrugineus* and to 'recreate' this rare wetland type, three new populations were established at Lake Serpentine, Lake Komakorau, and Waiwhakareke between 2006 and 2008 (Peters, 2007; Fig. 1).

Houdinia flexilissima appears to have a 2-year life cycle, based on the presence of earlier instar larvae in stems at the time of adult emergence. Adults lay eggs in late spring (October–November) near the base of a scale-like leaf of *S. ferrugineus*. The larvae mine into the green photosynthetic layer of the stem leaving star-shaped excavation tunnels extending up the stem (Fig. 2). The larva of *H. flexilissima* represents one of the most modified (and certainly one of the thinnest) larvae of all Lepidoptera (Hoare *et al.*, 2006) and appears specialized for feeding on *S. ferrugineus*. Later instars burrow in the deeper tissues of the culm, showing no external sign of their presence. Although more than one egg and excavation tunnel are commonly observed on a single stem, only one larva has ever been found inside each stem. Despite this damage, the vigour of the plant seems unaffected (Hoare *et al.*, 2006). Pupation occurs in the internodes of the culms in a chamber lined with fine whitish silk, the exit-hole usually being just above a leaf. Adults hatch over spring (October–December). The behaviour of the pharate adult at eclosion is a mystery, because no pupal remains were found in or protruding from stems from which adults had emerged; however, most emergence holes are surrounded by a rim of shed scales. When reared, adults rested on the brownish leaves at the



Figure 1. Locations of *H. flexilissima* populations in the Waikato, New Zealand. There are three naturally occurring populations at Kopuatai, Moanatuatua and Torehape Reserve. In addition, there are translocated populations at Lake Komakorau, Lake Serpentine, Waiwhakareke, and on the naturally regenerated at Torehape peat mine.

internodes of the host culms and in this position were well camouflaged and extremely hard to detect (Hoare *et al.*, 2006).

The larvae of *H. flexilissima* are totally dependent on *S. ferrugineus* for shelter and food. For this reason, Stringer *et al.* (2012) recently classified *H. flexilissima* as threatened and also placed it within the 'relict' category as the moth is found naturally at only three locations within the Waikato. Despite the threatened status of *H. flexilissima*, little is known about its distribution, abundance or its autecology. The objective of this study was to assess the distribution and abundance of *H. flexilissima* in the three naturally occurring *Sporadanthus*-dominated peat bogs (Kopuatai, Torehape and Moanatuatua) and at the translocated and restored populations of *S. ferrugineus*. The study was designed to determine some of the habitat preferences of *H. flexilissima* and included an investigation into whether the abundance of *H. flexilissima* was correlated with plant nutrients. Finally, this study was also designed to test the suitability of a new sampling method for monitoring the species.



Figure 2. Larva, early excavation tunnel, and adult male of *Houdinia flexilissima* (Lepidoptera: Batrachedridae). The larvae of *H. flexilissima*, colloquially named 'Fred the Thread', feed in the green photosynthetic layer of *Sporadanthus ferrugineus* stems, leaving these characteristic tunnels. The adults are small delicate moths that are found in Waikato peat bogs between October and December.

METHODS

Study sites

Three naturally occurring peat bogs, Kopuatai (10201 ha), Torehape (350 ha) and Moanatuatua (114 ha), in the Waikato contain representative examples of the original restiad raised bog ecosystem. This typically comprises an upper tier of *S. ferrugineus* up to 2.5 m in height, which overtops a dense lower layer of intertwining wiry-stemmed *Empodisma*. Other common species include *Epacris pauciflora*, *Leptospermum scoparium* and *Baumea teretifolia*.

Mining for horticultural peat occurs at Torehape, but the operators are required to restore the original peat bog vegetation after the permitted depth of peat has been removed (usually 1 metre). The area of the peat mine is 150 ha, of which only 40 ha remain unmodified. Current recommended practice for restoration of mined areas involves the creation of raised 'habitat islands' (5 m diameter and 30 cm high) of processed peat approximately 30 m apart. These were seeded with the shrub *Leptospermum scoparium* (Myrtaceae), an early successional plant in peat bogs, which is eventually out-competed by *S. ferrugineus* (Clarkson, 2002). The islands reached 100% vegetation cover in 2 years, with late successional peat bog plants beginning to establish within this timeframe (Schipper *et al.*, 2002). All the islands within a 'lane' were of similar age and each 'lane' was approximately 45 m wide and 950 m long.

Three new populations of *S. ferrugineus* were established at Lake Serpentine, Lake Komakorau

and Waiwhakareke between 2006 and 2008 (Peters, 2007) by transplanting plants of between 0.5 and 1.5 m tall from Torehape peat mine to each site to achieve planting densities of approximately 0.75 plants per m² (Peters, 2007). At all the translocated sites, the existing vegetation (exotic pasture grasses and weeds) was removed and the upper soil layers excavated to a depth of 30 cm to form a shallow depression that was then filled with peat to a depth of *c.* 30 cm. Translocated plants were removed from Torehape peat mine and immediately taken to the translocated site. Areas planted were 20 × 9 m (180 m²) at Lake Komakorau, 30 × 9 m (270 m²) at Lake Serpentine and 22 × 12 m (264 m²) at Waiwhakareke. It was assumed that *H. flexilissima* would also be translocated within the *S. ferrugineus* plants (Peters, 2007).

Monitoring *H. flexilissima* in *Sporadanthus*-dominated peat bogs in the Waikato

At Kopuatai, Torehape and Moanatuatua, paired plots were established 10 m apart on opposite sides along a transect in vegetation dominated by *S. ferrugineus* (>75% cover) and at varying distances from the edge of the wetland (Table 1). Two transects at Kopuatai (Tee Canal and Northern transect) and one transect each at Moanatuatua and Torehape were established (Table 1).

At Torehape peat mine, three mined 'lanes' that had been restored 11, 13 and 15 years previously were chosen for study. The study 'lanes' were approximately 150 m apart, separated by drains and other 'lanes' that had been restored with peat islands of varying ages.

Table 1. Location of *H. flexilissima* surveys in Waikato wetlands.

Wetland	Transect location	Number of plots (n)	Distance of plots from wetland edge (m)
Kopuatai Wetland Reserve	Transect 1: Tee Canal	8	35, 70, 105, and 140
Kopuatai Wetland Reserve	Transect 2: Northern transect	6	500, 1000, and 1500
Moanatuatua Peat Scientific Reserve	Transect 1	10	5, 50, 100, 200, and 300
Torehape Wetland Management Reserve	Transect 1	6	25, 70, and 105

Table 2. GLM parameters for proportions of stems damaged per plot, number of larva per metre of stem and larval size (mm) of *H. flexilissima*.

Wetland	Parameter	F	P
Proportion of stems damaged per plot	Wetland×Distance	0.61	0.544
	Wetland	139.63	<0.001
	Distance	8.91	0.003
Number of larva per metre of stem	Wetland×Distance	0.25	0.779
	Wetland	112.15	<0.001
	Distance	19.69	<0.001
Larval size	Wetland×Distance	0.43	0.655
	Wetland	70.55	<0.001
	Distance	23.09	<0.001

At approximately 600 m from the adjacent wetland, two islands spaced approximately 20 m apart were surveyed for presence of *H. flexilissima* on naturally regenerated *S. ferrugineus* plants on these islands. One plot on each island was placed in vegetation dominated by *S. ferrugineus* (>75% cover).

At the translocated *S. ferrugineus* populations at Lake Serpentine, Lake Komakorau and Waiwhakareke, one plot was placed approximately 2 m inside each of the four corners of area of translocated *S. ferrugineus* populations.

Surveys were carried out from 25 March to 23 April 2013. At each sampling point, a GPS position was recorded then a 33 cm diameter circular frame (0.086 m²) used to define the plot was placed over the *S. ferrugineus*, and 20 stems were randomly chosen from within this plot. Each stem was sampled by removing a piece 60 cm long (measured from the first internode directly below the seedhead) and collecting it in a paper bag (800 × 400 mm) for later examination in the laboratory. In the laboratory, stems were searched for the presence/absence of *H. flexilissima* and dissected to count the larvae of *H. flexilissima*. The number of

larvae (alive, dead, or presence of frass) and larval size were recorded for each stem. The presence of external damage from stem-mining was used to calculate the proportion of stems damaged per plot. The width of each *S. ferrugineus* stem (mm) was recorded at 60 cm below the seedhead and the lowest and highest *H. flexilissima* excavation tunnel relative to the seedhead were recorded.

Plant nutrients in *S. ferrugineus* stems

Plant nutrients have been shown to decrease from the edge to the centre of Waikato peat bogs (Clarkson *et al.*, 2004) and we were interested in investigating whether *H. flexilissima* abundance was correlated with plant nutrients. At each sampling point, a subsample of six *S. ferrugineus* stems each measuring 4 cm in length was analysed for nitrogen, phosphorus, potassium, sulphur, calcium, magnesium, sodium, iron, manganese, zinc, copper, and boron. Means ± 95% CI were calculated for each plant nutrient at each wetland so that differences ($P = 0.05$) between wetlands were apparent by inspection.

Data analysis

The data from the naturally occurring populations of *H. flexilissima* (Kopuatai, Moanatuatua and Torehape) were analysed using a general linear model (GLM), testing the fixed treatment effects of wetland and distance from the wetland edge. Models with number of larvae per metre of stems and average larval size as response variables assumed a normal error distribution, models testing the proportion of stems damaged per plot used a binomial error distribution with a $\log_e(x+1)$ link function, and the model testing the proportion of stems damaged per plot used a binomial error distribution and a logit link function. An unpaired *t* test was used to compare the herbivory rates, density, and average larval size of *H. flexilissima* in naturally occurring *S. ferrugineus* areas with those in translocated areas. The relationship between the proportions of stems damaged per plot and the number of larvae per metre of stem was analysed using a simple linear regression. All statistical analyses were performed using GenStat version 8.1.0.152 (VSN International, 2012).

RESULTS

Distribution and abundance of *H. flexilissima* in *Sporadanthus*-dominated peat bogs in the Waikato

A total length of 600 m of *S. ferrugineus* stem from 50 plots was examined for the presence of *H. flexilissima*.

All the variables measured showed no significant interaction between wetland and distance from the wetland edge (Table 2). However, this is probably due to lower rates of herbivory, larval densities and larval size collected from Kopuatai (particularly at Tee Canal) compared with Moanatuatua and Torehape, where the data showed similar trends (Figs 3A, 4A, and 5A). The treatment effects of wetland and distance from wetland edge were both significant for the variables measured (Table 2). Moanatuatua and Torehape had similar intercepts and slopes whereas those for Kopuatai differed (Table 2, Figs 3A, 4A, and 5A). At Kopuatai, Moanatuatua and Torehape, herbivory rates, larval density, and larval size increased significantly with distance into the wetland (Table 2, Figs 3A, 4A, and 5A). The proportions of stems damaged per plot and larval densities were much lower, and smaller larvae were found in *S. ferrugineus* stems at Tee Canal in Kopuatai (Figs 3A, 4A, and 5A).

Overall, the herbivory rates, larval density and larval size of *H. flexilissima* did not differ

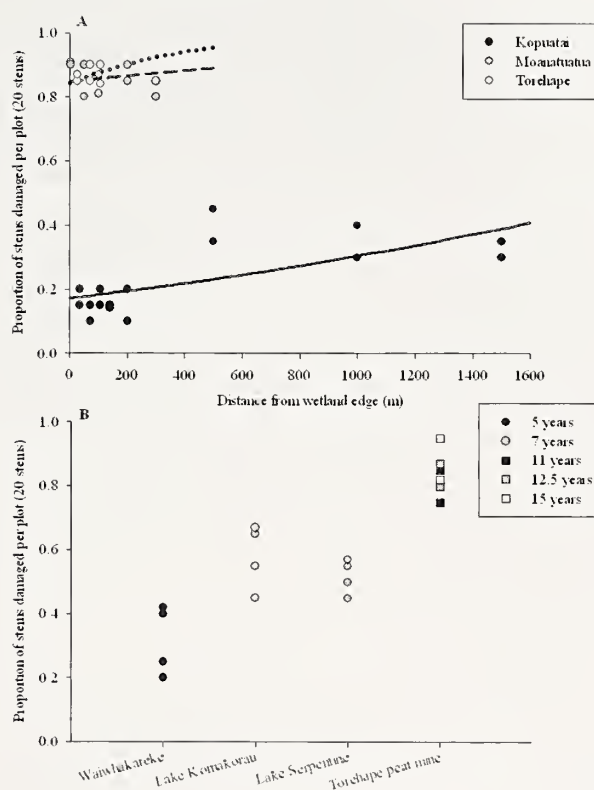


Figure 3. Proportion of *S. ferrugineus* stems damaged by *H. flexilissima*. **A)** Naturally occurring populations at Kopuatai, Moanatuatua and Torehape; **B)** Other locations, including translocated and restored populations. Equations of the fitted lines are Kopuatai (solid line) = $-1.585+0.000777x$; Moanatuatua (medium dashed) = $1.721+0.000745x$ and Torehape (dotted line) = $1.689+0.0027x$. Coincident data have been offset for clarity.

between the naturally occurring and translocated or restored populations (proportions of stems damaged, $t = 0.523$, $df = 1, 48$, $P = 0.603$; larval density, $t = 0.432$, $df = 1, 48$, $P = 0.667$; and larval size, $t = 0.457$, $df = 1, 48$, $P = 0.568$) of *S. ferrugineus*. There was some variation in herbivory rates, larval density and larval size of *H. flexilissima* at the translocated sites but this fell within the range observed in the naturally occurring populations. Herbivory rates, larval density and larval size of *H. flexilissima* were all similar at Lake Komakorau, Lake Serpentine, and Torehape peat mine whereas these were marginally lower at Waiwhakareke, the youngest population translocated 5 years ago (Figs 3B, 4B, and 5B).

The proportions of stems damaged per plot showed a significant positive relationship with the number of larvae found per metre of *S. ferrugineus* stem ($F_{1,49} = 332.37$, $P < 0.0001$; Fig. 6). Kopuatai had

a lower proportion of stems damaged per plot and number of larvae found per metre of stem compared with Moanatuatua and Torehape (Fig. 6). Values for the translocated populations and restored population of *S. ferrugineus* at Torehape peat mine fell within the values for Kopuatai (low) and Moanatuatua-Torehape (high) (Fig. 6).

Houdinia flexilissima was found in stems ranging from 1.62 to 4.46 mm in diameter and the average stem width for *S. ferrugineus* stems at 60 cm below the seedhead was similar across all the wetlands surveyed (Fig. 7). In addition, the stem width where the lowest and the highest excavation tunnel of *H. flexilissima* were found was similar in all wetlands (Fig. 7). The average stem width where the lowest excavation tunnel was found was consistently larger than the stem width where the highest excavation tunnel was found (Fig. 7).

Plant nutrients in *S. ferrugineus* stems

No differences in the nutrient concentrations of *S. ferrugineus* stems were detected between the wetlands sampled except for manganese and iron. Manganese had a significantly higher concentration at the translocated populations at Waiwhakareke, Lake Komakorau and Lake Serpentine than elsewhere (Fig. 8) and iron had a significantly higher concentration at Tee Canal in Kopuatai than elsewhere (Fig. 9).

DISCUSSION

Houdinia flexilissima was found in all the peat bogs where *S. ferrugineus* occurs in the Waikato but it is particularly encouraging, from a conservation perspective, that this moth has established, and populations appear to be viable at the translocated *S. ferrugineus* populations at Lake Komakorau, Lake Serpentine, Waiwhakareke, and where *S. ferrugineus* plants have naturally regenerated at the restored Torehape peat mine. A review by Schultz *et al.* (2008), found that most conservation strategies for threatened butterflies recommended reintroduction ($n = 34$) which has been attempted for 21 British species and only 5 American. Documentation of reintroduction techniques and whether the translocations were successful was limited. The present study confirmed that no additional intervention is required for translocating *H. flexilissima* other than translocating *S. ferrugineus* plants containing *H. flexilissima* larvae. This moth was translocated to Waiwhakareke only 5 years ago and so is probably still in the establishment phase and we suggest this might be why the herbivory rates and larval density were marginally lower and

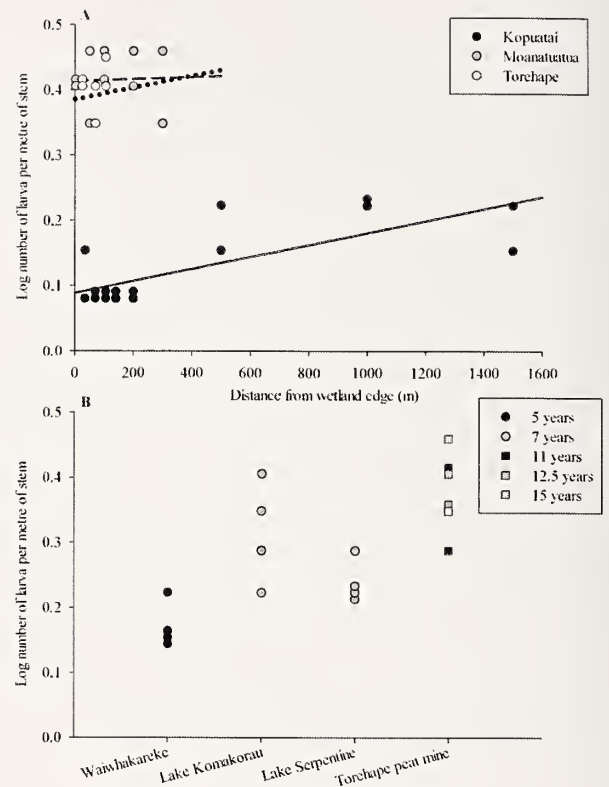


Figure 4. Number of *H. flexilissima* larvae per metre of *S. ferrugineus* stems. **A)** Naturally occurring populations at Kopuatai, Moanatuatua and Torehape; **B)** Other locations including translocated and restored populations. Equations of the fitted lines are Kopuatai = $0.0886 + 0.0000926x$, Moanatuatua = $0.4132 + 0.000016x$, and Torehape = $0.3855 + 0.0000907x$. Coincident data have been offset for clarity.

larvae were smaller than in the other two translocated populations which were transferred 2 years earlier. It is expected that the herbivory rates, larval density, and size of *H. flexilissima* will be similar to the other translocated populations within the next few years.

We can offer no explanation as to why herbivory rates, larval density, and larval size increased significantly with distance into the wetland in the larger areas (> 350 ha) of naturally occurring populations of *S. ferrugineus* but herbivory rate and larval density appear not to be related to dispersal ability of the moth as evidenced by the experimental work of Watts & Didham (2006). They found that wetland habitat loss at the Torehape peat mine caused an almost complete failure of *H. flexilissima* to colonise potted *S. ferrugineus* plants at distances of greater than 400 m from undisturbed wetland and that the number of eggs and larvae in *S. ferrugineus*, and the proportion of *S. ferrugineus* stems damaged,

all decreased logarithmically with increasing distance from the intact wetland habitat, and this was presumably due to limitation in the dispersal ability of the herbivore. They also found that average larval size decreased logarithmically with increasing distance from the intact wetland habitat but offered no explanation for this. Yet, recolonisation was surprisingly rapid following experimental habitat restoration. Three years after restoration there was no significant difference in the frequency of oviposition in host plants at differing distance of isolation from the wetland, and 6 years after restoration, the degree of herbivory damage had returned to pre-habitat loss levels (Watts & Didham, 2006).

The largest area of *S. ferrugineus* in the Waikato occurs at Kopuatai Wetland Reserve (10, 201 ha). However, the herbivory rates, density of larvae, and larval size of *H. flexilissima* were significantly lower here than at the other wetland sites. One possible factor may be the influence of plant size which could make larger plants more visible, emit more volatiles that attract adult moths or provide more resources for oviposition (thus increasing colonisation rate). Furthermore, it is widely accepted that larger host-plant patches will have a higher probability of establishment success and a lower risk of population extinction than smaller host-plant patches, for any given colonisation rate. Plant size was not measured in the study but it is unlikely that the plants at Kopuatai were smaller than at the other wetlands.

One possible reason why herbivory rates and density of larvae were lower, and larvae were smaller at Kopuatai could be related to nutrient levels within the *S. ferrugineus* plants but we detected no differences between the wetlands except for manganese which was higher in the translocated locations than elsewhere and for iron that was higher at Transect 1 (Tee Canal) in Kopuatai than elsewhere. It is unknown why these differences are present although the presence of a nearby freshwater spring at Tee Canal may relate to the higher concentrations of iron there but we did not sample the water. It is also unknown what effect these differences in concentration might have on *H. flexilissima*. The only information relating to nutrient levels for manganese or iron and Lepidoptera was published by Phelan *et al.* (1995) who found oviposition rates of the European corn borer, a pyraloid moth (*Ostrinia nubilalis*), were positively correlated with iron. However, interactions between minerals, other nutrients and ecological factors may be variable and be more important than single measures but remain unknown.

The proportion of stems damaged per plot showed a positive relationship with the number of larvae per

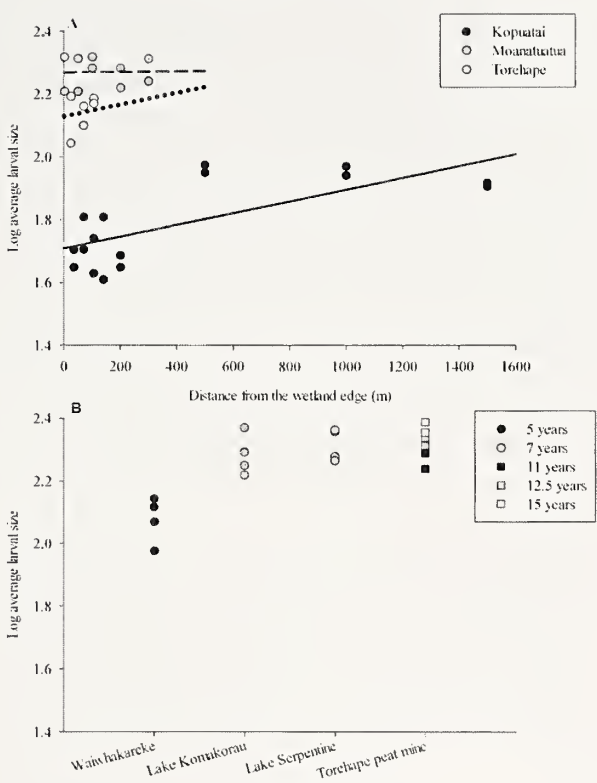


Figure 5. Average larval size (mm) of *H. flexilissima*. **A)** Naturally occurring populations at Kopuatai, Moanatuatua and Torehape; **B)** Other locations including translocated and restored populations. Equations of the fitted lines are Kopuatai = $1.707+0.000190x$, Moanatuatua = $2.268+0.0000095x$, and Torehape = $2.129+0.000186x$. Coincident data have been offset for clarity.

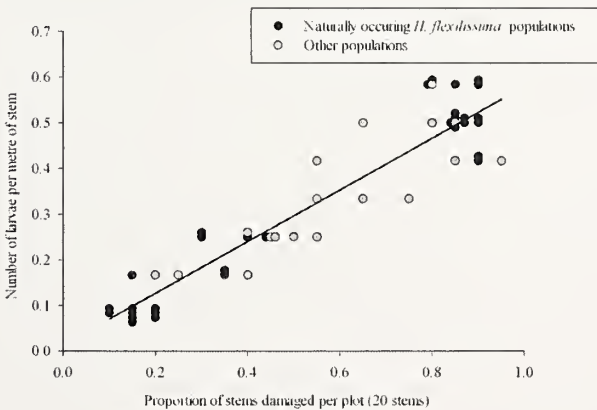


Figure 6. Relationship between the proportions of stems damaged per plot and the number of larvae per metre of stem. Regression equation is $y = 0.0136+0.565x$. Coincident data have been offset for clarity.

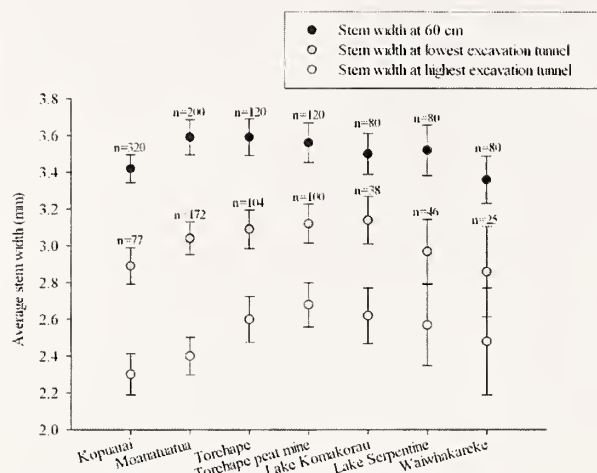


Figure 7. Average width of *S. ferrugineus* stems measured and stem width at highest and lowest excavation tunnel of *H. flexilissima*. Means \pm 95% CI are presented so that any differences ($P = 0.05$) between wetlands are apparent by inspection. Upper n = number of stems measured at 60 cm at each wetland, lower n = number of stems measured at lowest/highest excavation tunnel at each wetland.

metre of stem demonstrating that the proportion of stems damaged can be used as a surrogate for the number of larvae per metre of stem as it provides similar information on the overall abundance of *H. flexilissima* present in a *S. ferrugineus* plant. Stems, therefore, do not need to be harvested from the *S. ferrugineus* plant in the peat bogs and dissected to record the number of larvae so using the proportion of stems damaged avoids the killing of larvae of a threatened species. Our procedure whereby 1000 stems of *S. ferrugineus* were harvested resulted in the deaths of 198 *H. flexilissima* larvae, because they cannot survive once removed from the *S. ferrugineus* stems.

From this study, *H. flexilissima* can survive wherever there are *S. ferrugineus* plants. The moth appears to have established and be thriving even in the small (≤ 270 m²), translocated populations. Our results suggest that *H. flexilissima* appears to have a preference for *S. ferrugineus* stems between approximately 2.0 and 4.5 mm in diameter based on the amount of herbivory that stems in this size range experience. Adult *H. flexilissima* moths appear to target this size of stem to lay their eggs, and we speculate that it may be easier for first instar larvae to mine into the green photosynthetic layer of smaller, younger stems compared with older stems which are more rigid.

One of the greatest possible threats facing Waikato peat bogs is weed invasion, particularly in areas of fertile sedgelands and rush lands surrounding the

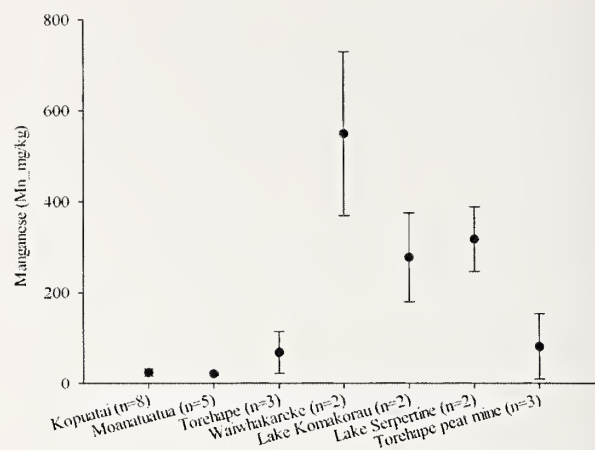


Figure 8. Concentrations of manganese (mean \pm 95% CI) found in *S. ferrugineus* stems collected from Waikato wetlands.

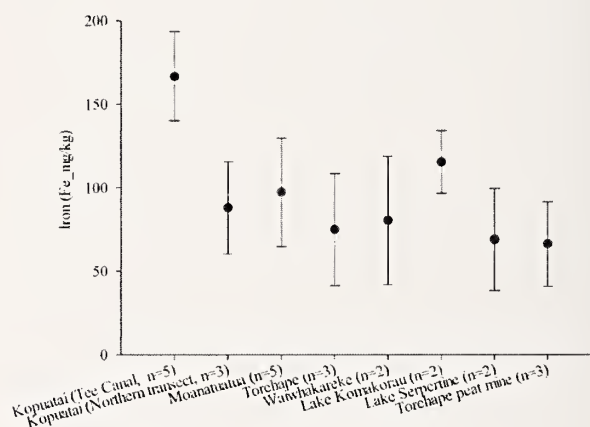


Figure 9. Concentrations of iron (mean \pm 95% CI) found in *S. ferrugineus* stems collected from Waikato wetlands.

nutrient-poor raised bogs dominated by *S. ferrugineus*. For example, willow (*Salix* spp.) and *Osmunda regalis* have become increasing components of the sedge-dominated vegetation at the higher-nutrient margins of Waikato peat bogs such as Kopuatai. A recent study in Waikato wetlands indicates that introduced grey willow (*Salix cinerea*) appears to dramatically alter the composition of beetle communities present. However, these communities can be restored to a beetle fauna that is similar to those found within native wetlands through willow removal (Watts *et al.*, 2012).

This sampling method could be applied to ecological studies investigating other stem-boring Lepidoptera associated with other plant species and

would be a particularly useful method for other threatened species. In New Zealand, in addition to *H. flexilissima*, there are a number of stem-boring species of Lepidoptera that are restricted to peat bogs. For example, the larvae of *Bactra* sp. (Tortricidae) feed in the stems of *Empodisma minus* and '*Batrachedra*' sp. near *eustola* (Batrachedridae) larvae mine in the stems of *Baumea teretifolia* (Hoare *et al.*, 2006). These are potentially of conservation concern because their distribution, abundance and habitat requirements remain unknown.

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A new *Entheus* (Hesperiidae: Eudaminae) from Colombia and Panama is most distinctive in the *E. gentius* group

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Abstract. A new species of *Entheus* is described from the Magdalena Valley in Colombia (type locality) and Panama. *E. huertasae*, **sp. nov.** stands out from other species in the *E. gentius* group by the black posterior half on ventral hindwing, the placement of spots in the apical yellow band on the forewing, width of hindwing black margin, mostly yellow anal fold, characters of the male genitalia, such as penis shape and length of tegumen processes, and about 7% difference in DNA barcode sequence. Identification key to males in the *E. gentius* group is given, and difficulties with *Entheus* taxonomy are discussed.

Resumen. Se describe una nueva especie de *Entheus* habitante del Valle del río Magdalena en Colombia (localidad tipo) y Panamá. *E. huertasae*, **sp. nov.** se distingue de las otras especies del grupo *E. gentius* por tener la mitad posterior negra en las alas posteriores ventrales, por la disposición de puntos en la banda amarilla apical de las alas anteriores, por el ancho del margen negro de las alas posteriores, por el pliegue anal que, en su mayor parte, es amarillo, por las características de los genitales masculinos como la forma del pene y la longitud de los procesos de tegumen, y la diferencia de aproximadamente el 7% en la secuencia de código de barras de ADN. Se presenta una clave para identificar los machos del grupo *E. gentius*, y se analizan algunas dificultades en la taxonomía de especies de *Entheus*.

Key words: new species, taxonomy, Neotropical, skipper butterfly, cryptic species, field marks, COI, mitochondrial DNA.

INTRODUCTION

The genus *Entheus* Hübner, [1819] includes over a dozen showy skipper species visually characterized by a contrasting combination of black, white, yellow and orange colors (Warren *et al.*, 2013). Its comprehensive synonymy and bibliography are provided by Mielke (2005), species groups are discussed by Grishin (2012) and all recognized taxa and many extant primary types are illustrated in Warren *et al.* (2013). *Entheus* is notorious for extreme sexual dimorphism that renders confident sex association by appearance nearly impossible; and

for taxonomic hardship caused by the loss of primary types for several difficult to recognize taxa, presence of many cryptic species, and curious for many HesperIIDae: Eudaminae similarity of male genitalia even in very distantly related species (Evans, 1952; Steinhauser, 1989; Austin *et al.*, 1997; Austin, 1997; Janzen *et al.*, 2011; Grishin, 2012). Interestingly, *Entheus* female genitalia offer an array of diagnostic characters and are frequently more distinct than male genitalia (Austin *et al.*, 1997; Steinhauser, 1989), but their potential power in *Entheus* taxonomy is yet to be realized, partly due to the difficulties with sex associations. Adults are secretive, routinely perching concealed on lower leaf surfaces in shady wooded areas (similarly to many Riodinidae), and many species are very rare in collections, exacerbating taxonomic puzzles.

The first glimpse into the hidden diversity of cryptic species in *Entheus* was given by Steinhauser, Austin and Mielke (Steinhauser, 1989; Austin *et al.*, 1997; Austin, 1997). Spectacular work by Janzen and colleagues in rearing of many dozens of *Entheus* specimens from caterpillars collected in the wild in the Area de Conservación Guanacaste (northwestern

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Costa Rica), followed by careful analysis of their foodplants, wing patterns, genitalia and mitochondrial DNA COI barcode snippets, re-iterated this notion (Janzen *et al.*, 2011). For instance, Janzen *et al.* (2011) reported and illustrated three likely undescribed *Entheus* species from the *E. matho* Godman & Salvin, 1879 group. These three species are close to each other in facies and are very similar in genitalia, yet they differ significantly in larval food plants and ecology. Their DNA barcodes are also slightly but consistently divergent. Thus, they likely represent distinct sympatric species and exemplify cryptic species diversity in *Entheus* that has also been revealed through traditional taxonomic methods (Austin *et al.*, 1997; Austin, 1997). The three cryptic *E. matho* group putative species, presently termed “Burns01”, “Burns02”, and “Burns03”, offer valuable clues about phenotypic differences in *Entheus* that may be indicative of species-status versus individual variation, and provide definitive male-female associations in taxa displaying marked sexual dimorphism.

While it might seem imprudent to approach *Entheus* taxonomy in any way short of a comprehensive revision fully addressing the name-bearing types to define the identities of existing names, it is also important to characterize the biodiversity and name newly discovered species in timely fashion. Such an approach to the problem (one bit at a time) has been taking place (Austin *et al.*, 1997; Austin, 1997; Grishin, 2012). Due to the scarcity of many *Entheus* species, some of these were described from a single specimen. While this tactic has a higher risk in coining an unnecessary synonym and certain potential for creating future taxonomic problems, it attracts researchers and butterfly enthusiasts to these unique phenotypes with all likelihood representing distinct biological species and facilitates further studies. This, when done with due diligence, should be preferred to placing an unusual specimen in “taxonomic limbo” for years with hopes to obtain a series at some later point. For instance, after I named *E. warreni* Grishin 2012 from a single specimen, Ernst Brockmann (pers. comm.), prompted by the description, found another *E. warreni* specimen (illustrated in Warren *et al.*, 2013), which otherwise might have remained unnoticed (i.e. simply dismissed as “*E. matho*”) for years to come. Moreover, this specimen has been barcoded by the BOLD project (Ratnasingham & Hebert, 2007), and further analysis of this distinctive species is now possible, including a segment of its DNA sequence.

Here, I build on the work of Austin *et al.* (1997), who clarified the identity of *E. gentius* (Cramer, 1777) by designating a neotype and described two new species similar to *E. gentius* in appearance: *E. bombus*

Austin, Mielke & Steinhauser, 1997 and *E. aureolus* Austin, Mielke & Steinhauser, 1997. These three species comprise the *E. gentius* group. I describe a fourth species, characterized by unique wing patterns and genitalia features that represent a mixture of characters of the three named species, and discuss similarity and variation in *Entheus* and its relevance for delineation of *Entheus* taxa in light of available DNA barcode data. Possibly due to extreme sexual dimorphism, I was not able to find and associate any females with the males of this new species, therefore females are not discussed in this study.

MATERIALS AND METHODS

Entheus specimens were examined in the following collections: American Museum of Natural History, New York, NY (AMNH); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Natural History Museum, London, UK (BMNH); Museum für Naturkunde, Berlin, Germany (ZMHB); McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL (MGCL); Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Academy of Natural Sciences Philadelphia Collection, Philadelphia, PA (ANSP); Senckenberg Museum für Tierkunde, Dresden, Germany (MTD); Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (DEI); and Texas A&M University Insect Collection, College Station, TX (TAMU). Photographs by Ernst Brockmann of primary types in the Universidade Federal do Paraná, Curitiba, Brazil (DZUP) collection were also examined. Standard entomological techniques were used for dissection (Robbins, 1991), i.e. distal part of adult abdomen was broken off, soaked for 40 minutes (or until ready) in 10% KOH at 60°C, dissected and subsequently stored in a small glycerol-filled vial on the pin under the specimen. Genitalia and wing venation terminology follows Steinhauser (1981) with modifications. Length measurements are in metric units and were made from photographs of specimens taken with a scale and magnified on a computer screen. Photographs of specimens and dry genitalia were taken by the author with a Nikon D800 camera through a 105 mm f/2.8G AF-S VR Micro-Nikkor lens; dissected genitalia were photographed in glycerol with Nikon D200 camera without lens through microscopes at 4x, 5x, and 6.4x magnifications. Images were assembled and edited in Photoshop CS5.1. Genitalic photographs were taken in several focus slices and stacked in Photoshop to increase depth of field.

DNA was extracted and isolated using Macherey-Nagel (MN) NucleoSpin® tissue kit following the

manufacturer's protocol. An abdomen (intact, and used for genitalia dissection after DNA extraction) or a single leg (cut by scissors into small pieces) were lysed in 90 μ l MN T1 buffer with 12 μ l MN Proteinase K (22 mg/ml) by overnight incubation at 56°C. DNA was eluted to the final volume of 120 μ l (DNA concentration varied from 0.03 to 0.4 ng/ μ l). Barcode region was PCR-amplified in two segments (307, 408 bp) using the following sets of primers: LepF (forward, 5'-ATTCAACCAATCATAAAGATATTGG-3') – MLepR (reverse, 5'-CCTGTTCCAGCTCCATTTTC-3') and MLepF (forward, 5'-GCTTTCCCACGAATAAATAATA-3') – LepR (reverse, 5'-TAAACTTCTGGATGTCCAAAAAATCA-3'). Each PCR reaction contained 8.4 μ l of DNA template (for concentrations below 0.4 ng/ μ l, or volume needed to supply approximately 3 ng of DNA plus molecular biology grade water up to 8.4 μ l), 0.8 μ l of each primer (12.5 μ M) and 10 μ l Invitrogen AmpliTaq Gold 360 master mix. PCR products were cleaned using MN NucleoSpin® Gel and PCR Clean-up kit and eluted to the final volume 20 μ l. PCR products were sequenced from either MLepR (for the 307 bp segment) or MLepF (for the 408 bp segment) primers using Applied Biosystems Inc. (ABI) Big Dye Terminator 3.1 kit on ABI capillary instrument in the DNA Sequencing Core Facility of the McDermott Center at UT Southwestern. Sequence trace files were visualized in FinchTV and full barcode was manually assembled from the two segments in a text editor.

Additional DNA sequences were downloaded from GenBank (<http://genbank.gov>), aligned by hand since they matched throughout the length without insertions or deletions, and analyzed using the Phylogeny.fr server (<http://www.phylogeny.fr>) with default parameters (Dereeper *et al.*, 2008). Many of these sequences have been reported in Janzen *et al.* (2011) and photos of specimens are available from the Area de Conservación Guanacaste (ACG) on-line database (Janzen & Hallwachs, 2013) and BOLD database (Ratnasingham & Hebert, 2007) to confirm or suggest identification.

RESULTS

Selecting specimens for photography in the AMNH collection, among *E. gentius*-group males I noticed an *Entheus*, mounted ventral side up, with a broadly black instead of yellow-orange posterior hindwing, a character not observed in other species of the group. This specimen also appeared slightly larger than a typical male. A more careful inspection revealed other unique aspects and prompted a genitalic dissection. Comparison with the named *Entheus* species and analysis of their variation and

diagnostic traits suggested that this specimen belongs to an undescribed species, which appears to be more distinct from others in the *E. gentius* group. This new species is named here.

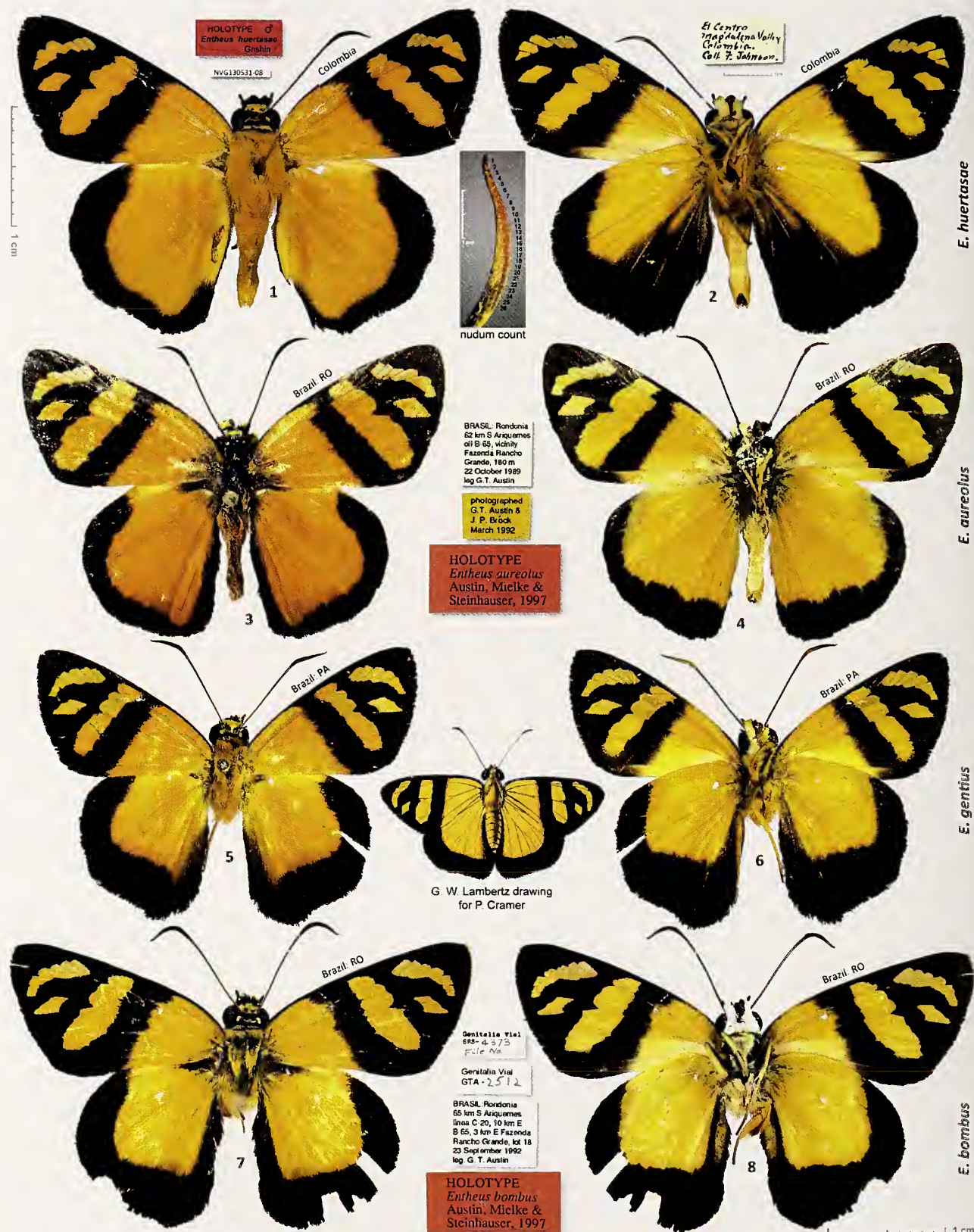
Entheus huertasae Grishin, new species

(Figs. 1–2, 9–26, 27a, 28 part, 29 part)

Description. *Male* (Figs. 1–2 & 9–24): right forewing length = 20 mm in holotype (for all ten type series specimens mean = 20 mm, standard deviation = 1 mm, range = 18.5–21 mm). **Forewing** elongated, triangular, apex pointed, not produced, outer margin convex, straighter near the tornus. **Dorsal forewing** black marked with yellow-orange: yellow-orange basal third; yellow-orange discal band from vein Sc to the middle of CuA₂-2A cell, edges irregular, almost parallel, band constricted along the cubitus; rhomboidal orange-yellow spot in cell M₃-CuA₁ closer to outer margin than to the base of the cell, spot separated from the discal band; six conjoined subapical spots between R₂ and M₃, spots separated from the discal band, three spots closer to costa hyaline (the only hyaline areas on wings) and in most specimens offset basad along R₅ relative to the other three spots. **Ventral forewing** pattern similar to dorsal, yellow-orange areas paler especially in CuA₂-2A and 2A cells; 2A cell pale-yellow except distal quarter. **Hindwing** slightly angled at M₃, with a hint of anal lobe at 2A. **Dorsal hindwing** yellow-orange with a black margin narrowing from covering distal third of cells near apex to the width of anal fold at tornus; basal half of anal fold yellow-orange in most specimens, slightly paler than the wing ground color, but overscaled black almost from the base in some specimens. **Ventral hindwing** yellow-orange with the black margin broader than on the dorsal side widening from between veins M₂ and M₃ to tornus; hindwing black in posterior half posterior CuA₁ with some yellow-orange overscaling at the bases of cells (especially in CuA₂-2A) and the base of anal fold. **Fringes** black, the same color as wing margins. **Head** yellow-orange above, two small black spots between the eyes near palpi, two large conjoined black spots between antennae and a black narrow band between the eyes, eyes dark-grayish-brown, framed with black scales; collar yellow-orange with a posterior belt of black scales; palpi black above, pale-cream below, last segment black with some yellow scales below; antenna black with yellow scales below mostly near and along the club, nudum of the right antenna of the holotype of 26 segments (nudum of 25, 26, 26, 26 and 27 segments in five paratypes). **Thorax and abdomen** yellow-orange above, thorax yellow-orange below with areas of black scales near the legs, abdomen pale yellow below; legs yellow-orange, hind tibial tufts (best seen in Fig. 12) with inner portion yellow-brownish, extending distad to near 3/4 length of first tarsomere, outer portion pale-brown with darker, brown tip (1/4 to 1/2 outer portion length) and short, extending distad 1/3 to 1/2 length of first tarsomere.

Male genitalia (Figs. 26 and 27a): typical for the group, tegumen narrower in lateral view than in other species from the *E. gentius* group, with two long and slender caudal processes that nearly reach the distal end of uncus; uncus longer than in *E. aureolus*, dorsally straight in lateral view with a caudal notch, uncus arms narrower and longer than those of *E. gentius* and *E. bombus*, more similar to those in *E. aureolus*; valva narrower than in other species from *E. gentius* group, costal process of valva reaches into the harpe; aedeagus narrower and less bulbous than in *E. gentius* and *E. bombus*, with longer phallobase, most similar to that of *E. aureolus*, with 10 spike-like cornuti in the holotype: 1 very long, 2 long and 3 slightly shorter than others. The exact number of cornuti is variable (as in other species) and is 13 in one paratype.

Female: unknown or unrecognized.



Types. Holotype male, mounted ventral side up, with the following labels: white, handwritten in black ink: / El Centro / Magdalena Valley / Colombia. / Coll. F. Johnson. /; white, printed: / NVG130531-08 /; red, printed: / HOLOTYPE ♂ / *Entheus huertasae* / Grishin /. A vial with genitalia is pinned under the specimen above the labels. The holotype is in the collection of the American Museum of Natural History, New York, NY (AMNH). Nine paratypes, all males from Panama: one from Colón Prov., Río Guanche, 17-Jan-1976, leg. G. B. Small, specimen number OM. 45.496; five from Panamá Prov.: Distrito de El Llano, Cordillera de San Blas, north of El Llano, ca. 330 m, (three of these specimens have "5mi N El Llano" and "9° 17'N 79° 00'W" on the labels), 19-May- and [5, 6, 8, 14]-Jun-1978, leg. G. B. Small (DNA extraction codes are NVG-1759, NVG-1782 and NVG-1784 for those collected on 19-May, 8-Jun and 6-Jun, respectively); one from Panamá Prov., Cerro Jefe, 490 m, 24-Sep-1973, leg. G. B. Small, DNA extraction NVG-1784; one from Veraguas Prov., near Punta Mariato, 800 m, 7° 13'N 80° 53'W, 12-Feb-1982, leg. G. B. Small; and one from Darién Prov., Darién National Park, Rancho Frio, 08° 01' 11.3"N 77° 43' 57.0"W, 100 m, 22-Jul-2013, leg. A. Thurman. The paratype from Colón Prov. is in the research collection of Olaf H. H. Mielke (Curitiba, Brazil) and the paratype from Darién Prov. is in the research collection of Albert Thurman (Phoenix, Arizona, USA), all other paratypes are in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Type locality. Colombia: Santander department, Magdalena River Valley, 18 air km southeast of Barrancabermeja, El Centro, GPS coordinates about 6° 56'N 73° 45'W, elevation 100-150 m.

DNA barcode sequences. Paratype from Panama: Panamá Prov., Distrito de El Llano, Cordillera de San Blas, N of El Llano, 330 m, 19-May-1978, leg. G. B. Small, genitalia vial No. NVG131129-01, DNA extraction NVG-1759 (Figs. 9–10), GenBank Accession KF921081, 658 base pairs:

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AACCTTATATTTTATTTTGGGAATTGAGCAGGAATGGTAGGTACT
TCTTTAAGATTACTAATTCGAAGTGAATTAGGAAGTCCAGGAT
CATTAATTGGCGATGATCAAAATTTATAACTATTGTAAGTCA
CATGCTTTTATCATAATTTTTTTTATAGTTATGCCAATTATAATT
GGCGGATTGGAAATTGATTAGTTCCTTTAATATTGGGAGCTC
CCGATATAGCTTTCCCTCGTATAAATAATATAAGTTTTTGACTTT
TACCCCATCATTAACATTATTAATCTCAAGAAGAATTGTTG
AAAATGGGGCCGGAACAGGATGAAGTGTATCCCCCATTATCTG
CTAATATCGCACATCAAGGTTCTTCAGTAGATTTAGCAATTTTTTCC
CTACATTTAGCTGGAATTTCTATCTATTTAGGAGCTATTAATTTT
ATTACAACAATTTATTAATATGCGAATTAGAAATTTATCTTTTGATC
AAATACCTTTTATCGTTTGAGCTGTAGGTATTACTGCTTTACTTTT
ATTATTATCTTTTACCTGTATTAGCTGGAGCTATTACTATATTATT
AACTGATCGAAATTTAAATACATCATTTTTTGATCTGCTGGAGGAGG
AGATCCAATTCTTTACCAACATTATTT
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Partial barcodes were obtained for three more paratypes: NVG-1782, NVG-1783 and NVG-1784 and deposited in GenBank with accessions KF921082, KF921083 and KF921084, respectively.

Two of these were identical in sequence to the full NVG-1759 barcode shown above, and NVG-1783 revealed 2 bp difference from it: position 100 T (not C) and position 181 T (not C), numbering from 1 to 658 for NVG-1759 sequence.

Etymology. It is my pleasure to name this new species in honor of Blanca Huertas, Curator of Lepidoptera, Natural History Museum, London, UK. Blanca's help has been instrumental in many projects dealing with Neotropical butterflies and skippers. Her diligence and hard work in helping researchers across the world, bit-by-bit, day after day has built up an admirable legacy. She is from Colombia and has a radiant, sunny and warm personality, a keen sense for recognizing talent, passion for butterflies and working with people, and a constant drive for excellence and accomplishing challenging projects. This beautiful, beamy and bright yellow-orange *Entheus* species, standing out due to its unique appearance, is also from Colombia and reminded me of her. The name is a feminine noun in the genitive case.

Distribution. The species is currently known from Panama (Colón, Panamá, Veraguas and Darién Provinces) and Colombia (Magdalena Valley) (Fig. 25) and has been recorded from forested areas at various low to mid-range elevations (100 to 800 m).

Diagnosis. The new species belongs to *Entheus* because it possesses the following characters used by Evans (1952) to circumscribe the genus: **A)** the third segment of palpi is stout and spatulate, positioned close to the outer edge of the second segment; **B)** antennae are bent at the beginning of nudum (i.e. segments with scaleless areas on antennal club), not distad of the beginning; **C)** forewing vein M_3 origin is in the middle between veins M_2 and CuA_1 , not twice as far from vein CuA_1 than from vein M_2 ; and **D)** it lacks a costal fold.

The new species belongs to the *E. gentius* group because: **a)** it has tuft of long scales on hind tibia (Fig. 2 & 9–24); **b)** its valva is with a long and slender costal process (Fig. 26); **c)** forewing spots and bands are yellow and not white; **d)** hindwing is largely yellow-orange and not entirely black or dark brown; and **e)** forewing is with a large rhomboidal spot in M_3 - CuA_1 cell (vs. narrow streak or no spot at all).

Using Evans (1952), the new species keys out to *E. gentius*, which was considered the sole species in this group by Evans. The neotype for *E. gentius* was designated by Austin *et al.* (1997), and two other species in the group: *E. bombus* and *E. aureolus*, were described. Austin *et al.* (1997) provided a key to *Entheus* males from their Rondônia study site, which keyed the new species to the choice between *E. aureolus* ("Yellow-orange, tuft on hind tibia with dark tip, VHW anal margin yellow", the holotype Figs. 3–4, 28 part) and *E. bombus* ("Yellow, tuft on hind tibia entirely yellow-orange, VHW anal margin black", the holotype Figs. 7–8, 28 part). The choice is inconsistent, because the new species can be described as "yellow-orange, tuft on hind tibia with dark tip, VHW anal margin black." However, according to Austin *et al.* (1997), this combination of characters refers to *E. gentius* (Figs. 5–6, 28 part), which has not been recorded from Central Rondônia and therefore not included in the key, but is re-described in detail in

Figures 1–8. (Opposite page) *Entheus gentius* group males. 1–2. *E. huertasae* n. sp. holotype, Colombia: Santander department, Magdalena River Valley, near Barrancabermeja, elevation 100-150 m (location data deduced from the label), genitalia vial No. NVG130531-08 (genitalia shown in Fig. 26); 3–4. *E. aureolus* holotype; 5–6. *E. gentius*, Brazil: Pará, Obidos, 1-Aug-1982, leg. Miers, OM 38.416, genitalia prep. Mielke 1994; 7–8. *E. bombus* holotype. Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. Magnified antennal club of *E. huertasae* holotype with nudum segments count is shown between the images of the specimen. G. W. Lambert drawing used as a basis for published engraving of *E. gentius* original description by P. Cramer (1777) is shown between the images of the specimen and is copyright (©) Trustees of the Natural History Museum, London (used with permission). Labels are shown for primary types in-line with the specimen images. Labels are reduced 2.5 times compared to specimens: small scale bar below *E. huertasae* locality labels refers to labels, and larger scale bars refer to specimens. 1–2 is in AMNH collection, other specimens are in DZUP collection and are photographed by Ernst Brockmann.



the text. The Austin *et al.* (1997) description of *E. gentius* additionally indicates: "portion in [forewing] discal cell hyaline (this latter appears to be a unique character for *E. gentius*)", dorsal hindwing "with very broad (nearly 1/3 wing width) black outer margin", "anal margin ... black", and "penis robust". The new species does not have hyalinity in the discal cell, its dorsal hindwing margin is much narrower, only slightly broader than that of *E. aureolus*, (Figs. 1–2 & 9–24) and aedeagus is narrow and slender (Figs. 26l, 27a) as in *E. aureolus* (Fig. 27b), and not stout as in *E. gentius* or *E. bombus* (Figs. 27c, d). Therefore, the new species exhibits a mixture of characters specified by Austin *et al.* (1997) for each of the three named species in the *E. gentius* group and does not fully agree with any of these three species.

A combination of the following characters sets the new species apart from all other *E. gentius* group species, with the first three characters being unique to it: **1)** ventral hindwing broadly black in posterior half, cells CuA_1 – CuA_2 and CuA_2 –2A are largely black, only with some yellow-orange overscaling basad (and not mostly yellow-orange in the basal half); **2)** three subcostal yellow-orange spots in the subapical band are usually offset basad (along R_5), relative to the three submarginal yellow-orange spots; **3)** hindwing anal fold dorsally yellow orange near the base in most specimens (tinged with black and brown in some); **4)** no hyalinity is present in discal cell, the only hyaline spots are the three subapical spots near costa, and not the usual four in other species of the *E. gentius* group; **5)** dorsal hindwing margin is narrowing from apex to tornus, only slightly broader than that in *E. aureolus*, and much narrower than that in the other two species; **6)** outer portion of tibial tuft short (extending distad 1/3 to 1/2 length of first tarsomere), pale brown, darker at the tip; **7)** penis narrow and slender, with long phallobase as in *E. aureolus*, not stout and bulbous as in other two species; **8)** tegumen narrower in lateral view than in other species; **9)** distal processes of tegumen long and slender, almost reach the distal end of uncus, as in *E. gentius* or *E. bombus*, but not shorter and broader as in *E. aureolus*; **10)** uncus longer and less angled than that of *E. aureolus*, dorsally straight with a caudal notch in lateral view; **11)** uncus arms narrow, like those in *E. aureolus*, not as stout as in the other two species; **12)** costal process of valva broadly curved as in *E. aureolus*, less straight than in other two species.

Variation. To illustrate variation, all but one paratypes are shown (Figs. 9–24) in addition to the holotype (Figs. 1–2). The contours of yellow orange discal forewing band varies, e.g. the band is strongly constricted along the cubitus in the holotype and some paratypes (e.g. Figs. 1 & 15), but is almost straight along basal edge in others (e.g. Fig. 13). The extent of offset in the apical forewing band is variable: the 3 hyaline spots by the costa may be very strongly offset basad compared to the three yellow orange submarginal spots (e.g. Figs. 1, 11 & 15), or almost aligned, especially along basal edge (Fig. 21). Anal fold dorsally, varies from mostly orange yellow in the majority of specimens, including the holotype (e.g. Figs. 1, 9, & 19) to almost brown (i.e. orange-yellow, overscaled with black-brown), except the very base (Fig. 23). The color of hind tibial tuft varies from paler yellow-brown to darker, almost brown, and the color of the tip could be from brown to almost black, but the tip is always darker than the base (compare Figs. 9–24).

DISCUSSION AND KEY TO MALES IN THE *E. GENTIUS* GROUP

The family Hesperidae offers an astonishingly broad array of possible evolutionary scenarios for the study of relationships between phenotype and genotype and their relevance to speciation. Quite a few species are easy to tell apart both by facies and genitalia, e.g. in genera *Myscelus* Hübner, [1819] and *Aethilla* Hewitson, 1868. A number of genera are well known for similarity in wing patterns, but genitalia are easily diagnostic for their many species, e.g. blue *Elbella* Evans, 1951, *Staphylus* Godman & Salvin, 1896, or *Erynnis* Schrank, 1801. The opposite scenario, when genitalia are alike and species can be more readily told apart by facies, is quite rare, but *Amblyscirtes* Scudder, 1872 comes to mind. This scenario is rare because, by definition, consistent differences in genitalia are typically viewed as an indication for species status (Burns, 2000; Austin & Warren, 2002). Therefore in the absence of notable differences in genitalia, hypothesizing about speciation is more difficult to support.

A fourth possible scenario can take place as well, when both facies and genitalia are similar and do not allow for confident placement of species boundaries. Such a conundrum was best revealed by the consorted analysis of life history data and a short snippet of genotype dubbed "barcode," which is a 654 base pair region of mitochondrial DNA encoding for the C-terminal segment of cytochrome c oxidase subunit I (COI). The best example is the skipper known as *Astraptes fulgerator* (Walch, 1775) which is likely an assembly of many cryptic species that at present cannot be identified with confidence by adult facies nor genitalia, but instead by caterpillar foodplants, patterns and ecology, and for many of them distinct DNA barcodes (Hebert *et al.*, 2004). *Entheus* belongs to the same skipper subfamily as *Astraptes* Hübner, [1819], and the studies of Janzen *et al.* (2011) revealed a similar situation in the "species" formerly identified as *E. matho* in collections. Three distinct *E. matho*-like species very similar in appearance and genitalia are sympatric in northwestern Costa Rica. A number of

Figures 9–24. (Opposite page) *Entheus huertasae* n. sp. paratypes. All are from Panama: **9–10 & 13–14.** Panamá Prov.: Distrito de El Llano, Cordillera de San Blas, N. of El Llano, 330 m, 19-May-1978, genitalia vial No. NVG131124-01, DNA NVG-1759 (**9–10**) and 6-Jun-1978 (**13–14**); **11–12.** Darién Prov., Darién National Park, Rancho Frio, 08° 01' 11.3"N 77° 43' 57.0"W, 100 m, 22-Jul-2013; **13–14.** Panamá Prov.: Distrito de El Llano, Cordillera de San Blas, N. of El Llano, 330 m 6-Jun-1978; **15–18 & 21–22.** Panamá Prov.: 5 mi N. El Llano, 9° 17'N 79° 00'W, 330 m, 5-Jun-1978 (**15–16**), 8-Jun-1978 (**17–18**) and 8-Jun-1978 (**21–22**); **19–20.** Panamá Prov., Cerro Jefe, 490 m, 24-Sep-1973; **23–24.** Veraguas Prov., near Punta Mariato, 800 m, 7° 13'N 80° 53'W, 12-Feb-1982. Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. A segment of a photograph with hind leg with tibial tuft is shown between specimen views. "F" indicates mirror image (left-right inverted). All specimens are in USNM collection and are leg. G. B. Small, but the one shown in **11–12**, which is leg. A. Thurman and is in the research collection of A. Thurman.

studies report close similarity in *Entheus* genitalia, even for species that are not very close to each other phylogenetically (Steinhauser, 1989; Austin *et al.*, 1997; Austin, 1997; Grishin, 2012). Some of these species are easier told apart by wing patterns than by genitalia (Austin *et al.*, 1997; Grishin, 2012). Thus, *Entheus* might be another example where wing pattern differences are more indicative of speciation than genitalia.

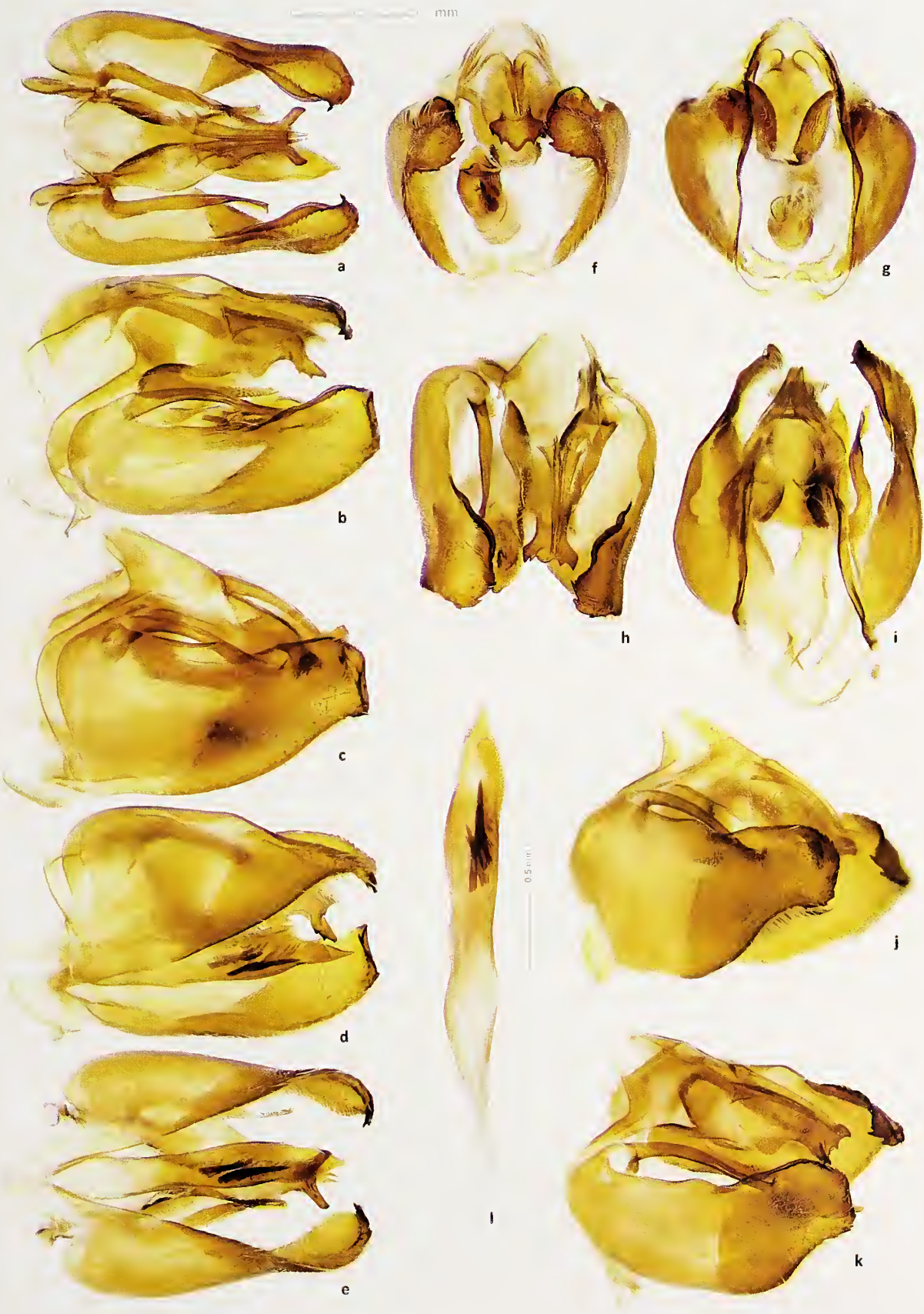
These results indicate the difficulties with *Entheus* taxonomy and evaluation of the status of proposed names. For instance, the three *E. gentius* group species, two of which were named by Austin *et al.* (1997), were all considered to be a variable single species by Evans (1952). On a casual look it is easy to dismiss moderate-at-best differences in wing patterns (Figs. 2-8, 28 part) and subtle differences in genitalia as intraspecific variation and synonymize these recently proposed names under *E. gentius*. However, available DNA barcode data strongly support Austin's *et al.* (1997) treatment (Fig. 29) and confirm that these differences, both in facies and genitalia, are indeed taxonomically meaningful. Despite general similarity in appearance, DNA barcode divergence between *E. aureolus* and *E. gentius* exceeds 7%, and is significantly larger than barcode divergence among the three undescribed Costa Rican species (1.1–2.3%), and almost twice as large as that between *E. priassus* (Linnaeus, 1758) and *E. crux* Steinhauser, 1989 (4%), which belong to different *Entheus* species groups, and were never considered to be very similar. The same refers to the comparison of *E. priassus* and *E. matho dius* Mabille, 1898 (5.2%). While a more detailed interpretation of extreme divergence between cryptically similar *E. aureolus* and *E. gentius* awaits further studies, it suggests that it is best to treat these taxa as distinct biological species. Divergence between *E. gentius* and *E. bombus* placed as sister taxa in the barcode tree in accord with similarity in their facies and genitalia (Fig. 29) is also substantial (4%) and is in agreement with their treatment as distinct species. As expected from morphology, DNA barcode confidently (90% bootstrap) groups *E. huertasae* n. sp. with *E. aureolus* (Fig. 29). Strongly supporting distinctness of *E. huertasae* as a species, the barcode difference from *E. aureolus* is quite large: 6.7%, and the difference exceeds 7% between *E. huertasae* and either *E. gentius* or *E. bombus*.



Figure 25. Map of *E. huertasae* n. sp. localities. Localities where specimens were collected are marked with black circles. Type locality is labeled "TL".

Such a high divergence in the *E. gentius* group is not likely explained by some errors in the data, because the tree topology (Fig. 29) is entirely consistent with the grouping by wing patterns, although many nodes in the tree lack statistical confidence due to barcode region being very short. For instance, this tree being rooted with the *Hyalothyrus neleus* (Linnaeus, 1758) sequence places *E. eunyas* Austin, Mielke & Steinhauser, 1997, which is a representative of the *E. eumelus* (Cramer, 1777) group, at the base of the tree consistently with the lack of costal processes on the valva and other characters that are likely to be synapomorphic for all other *Entheus* groups except the *E. eumelus* group. Next, all three species from the *E. gentius* group cluster together and are placed as a sister group to the rest of *Entheus* taxa, in accord with the Evans (1952) key arrangement. Finally, all species from the *E. matho* group (all remaining taxa except *E. priassus*) cluster together. Two other curious observations from this preliminary analysis are that *E. crux* is a sister of "Burns01": there is indeed a strong similarity in wing patterns of males, but females are very different (dark-brown hindwing vs. white with brown margin); and barcode of the recently described *E. warreni* is quite different from the rest (about 4%), supporting the proposed species status of this taxon named from a single specimen and confirming its placement in the *E. matho* group in agreement with wing pattern characters.

Figure 26. (Opposite page) *Entheus huertasae* n. sp. male genitalia, holotype. Genitalia vial No. NVG130531-08. Genital capsule in different views: a. dorsal; b. left dorsolateral; c. left lateral; d. left ventrolateral; e. ventral; f. posterior; g. anterior; h. dorsoposterior, slightly tilted to the right; i. dorsoanterior, slightly tilted to the left; j. left lateroposterior; k. left dorsolateroposterior. l. penis in ventral view, digitally removed from the genital capsule and edited. All images are to scale shown on the top, except l, which is magnified and a scale for it is given to the right.



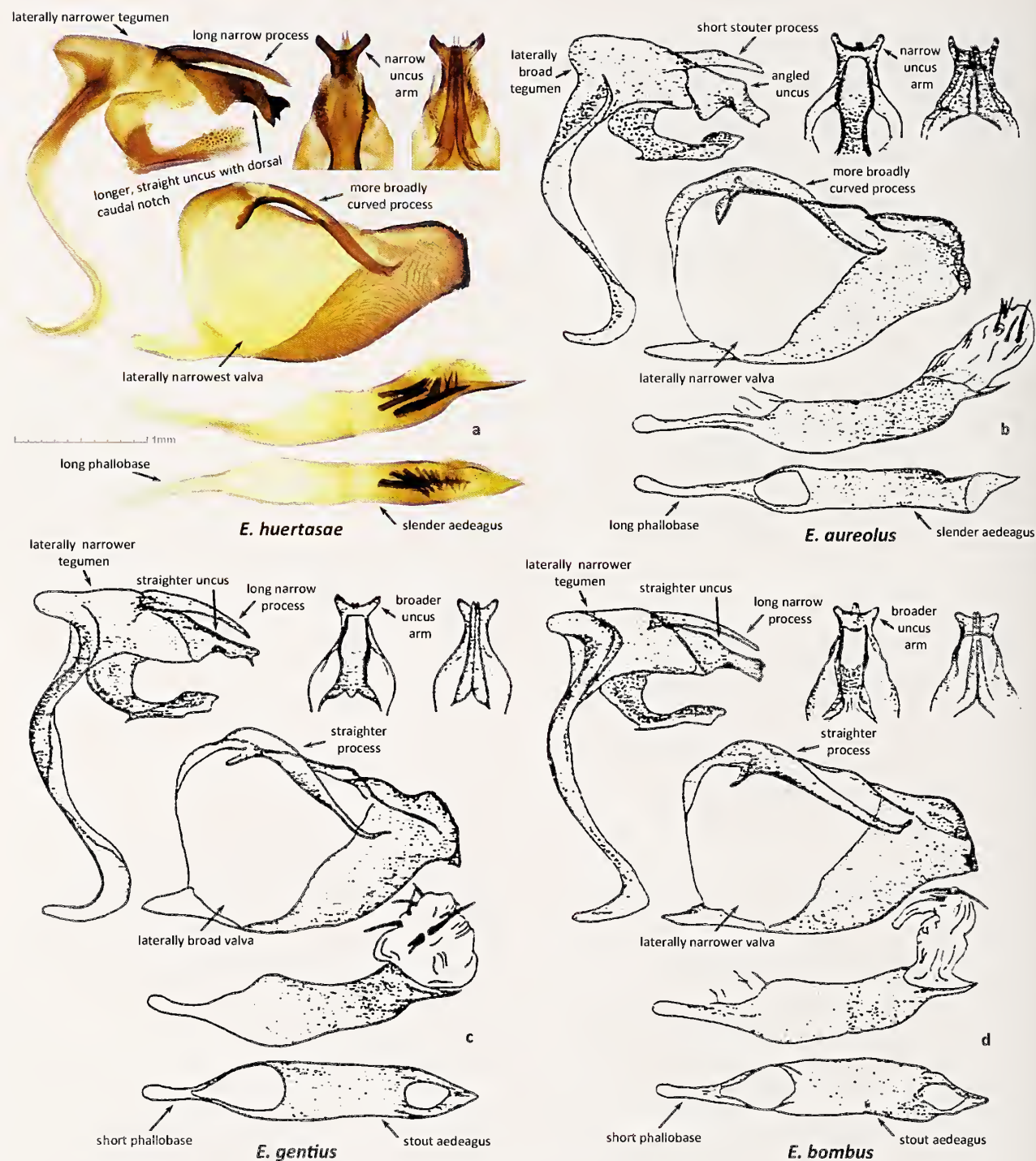


Figure 27. Male genitalia of species in *E. gentius* group. a. *E. huertasae* n. sp. paratype (genitalia vial NVG131124-01, specimen and data in Figs. 9–10); b. *E. aureolus* paratype, Brazil: Rondônia, 3 km E Fazenda Rancho Grande, lot 18, 22-Sep-1992 (GTA #2513); c. *E. gentius* neotype (GTA # 5766); d. *E. bombus* holotype (GTA # 2512). Images show lateral view of tegumen, gnathos, uncus, and associated structures; dorsal (on the right) and ventral (on the left) views of uncus, gnathos, and posterior tegumen; left lateral (above) and dorsal (below) views of penis (latter without vesica and cornuti on the drawing). "F" indicates mirror image (left-right inverted). The scale refers to photographs (a), the drawings (b–d) are scaled approximately and are reproduced with modifications from Austin *et al.* (1997), used with permission. Differences between species are indicated on the image.

While the barcode tree in this case is only confirmatory of existing taxonomic work based on traditional specimen analysis, it addresses the concerns about possible over-splitting in *Entheus* on the basis of seemingly minute characters that may not have biological relevance. Indeed, the barcode data suggest that *Entheus* is rich in cryptic species and small, but consistent features of wing patterns might be indicative of speciation. Correlating DNA divergence with phenotype, we can identify the characters that are more likely to be significant for species delineation rather than those that are caused by intraspecific variation. For instance, the width of the hindwing black margin, offsets in the subapical forewing band (revealed in Costa Rican undescribed species), robustness of aedeagus, shape of uncus in lateral view and length and shape of distal processes of the tegumen should be good characters to use. All these characters highlight the differences between *E. huertasae* n. sp. and the other three species in the *E. gentius* group.

The following key (see below) is proposed for the males of the *E. gentius* group species. The key is largely based on Evans (1952) and Austin *et al.* (1997), with minor modifications and the addition of *E. huertasae* n. sp. to

the group. *E. huertasae* is placed first and is immediately distinguished from the rest of the species due to its distinctive appearance and simplicity of recognition by the three unique easy to observe characters: 1) broadly black ventral hindwing in posterior half, 2) a triplet of forewing subapical spots offset along vein R_5 and 3) dorsally yellow (at least at the base in most specimens) anal fold. Therefore it will be the species that is the most straightforward to recognize both in dorsal and ventral aspects. However, DNA barcode (90% bootstrap in the NJ distance tree, Fig. 29), genitalia (more slender aedeagus and uncus arms, valva narrower in ventral view, more curved costal process of valva) and narrow hindwing margin of *E. huertasae* are more similar to *E. aureolus* than to the other two species. Therefore it is most likely that *E. huertasae* is a sister to *E. aureolus* rather than being basal to the group. I suggest the following linear order for the species in the *E. gentius* group that is expected to be phylogenetically meaningful: {(*gentius*, *bombus*), (*aureolus*, *huertasae* n. sp.)}. The two pairs in parenthesis are likely sister species. The characters that seem the easiest to observe are underlined in the key. Most pattern characters are illustrated in Fig. 28 and genitalia of type specimens compared in Fig. 27.

Key to the males of the *E. gentius* group species.

0. Hindwing largely yellow or yellow-orange with dark brown or black margin. Forewing spots and bands yellow or yellow-orange, sometimes at least partly hyaline closer to the apex and costa, but not white. Rhomboidal orange-yellow spot in cell M_2 - CuA_1 (not a narrow streak).....*Entheus gentius* group males
- 1a. Hindwing with a narrowing black margin dorsally near tornus, but ventrally broadly black in the posterior half, i.e. space from CuA_2 vein to anal margin almost entirely black and black scales are present in CuA_1 - CuA_2 cell from its base. Hindwing anal fold black ventrally and orange-yellow dorsally at least at the base in most specimens, but may be partly covered with dark scales. In the forewing subapical yellow-orange band, three anterior spots offset basad along vein R_5 from the three posterior spots. Forewing discal cell yellow spot without hyaline areas. Tuft on hind tibiae short, mostly pale brown with slightly darker tip. Orange yellow in color. Penis longer, more slender. Processes of tegumen long and narrow, reach the end of uncus. Panama, Colombia (TL: Magdalena Valley).....*E. huertasae* n. sp.
- 1b. Hindwing in some species may be with broad black margin dorsally, but ventrally largely orange-yellow except the dark marginal band and sometimes anal fold, i.e. cell CuA_2 -2A yellow orange at least in its basal half and the base of CuA_1 - CuA_2 cell yellow orange. Hindwing anal fold dorsally black or brown and ventrally may be yellow in some species. All six spots by the forewing apex in a smooth curve, or the distal edge of the curve with a weak basal offset of the anterior three spots compared to the three posterior spots; however, the basal edge either smooth, or with a more prominent distal offset of the two posterior spots (i.e. two submarginal spots in M_1 - M_2 and M_2 - M_3) and the spot in R_5 - M_1 aligned with the three anterior spots (in R_2 - R_3 , R_3 - R_4 , and R_4 - R_5) rather than with the submarginal spots. Forewing discal cell yellow spot may contain hyaline areas.....2
- 2a. Hindwing black margin narrow dorsally, narrowing towards the tornus, anal margin yellow ventrally (only fringes black), no hyaline areas in the forewing discal cell yellow spot. Tuft on hind tibiae short, with dark tip. Redder than other species, from orange yellow to orange in color. Aedeagus longer, more slender. Processes of tegumen shorter, more robust, end around 3/4 of uncus. Colombia, Peru, Venezuela (Amazonas), Brazil (north, TL: Rondônia), the Guianas.....*E. aureolus*
- 2b. Hindwing black margin broad, broadening towards the tornus. Anal margin black or with significant black overscaling ventrally. Hyaline areas in the forewing discal cell yellow spot in one of the species. Tuft on hind tibiae longer, entirely orange-yellow, or with dark tip. Aedeagus more stout. Processes of tegumen longer, almost reach the end of uncus.....3
- 3a. Yellow-orange spot in forewing discal cell with at least one hyaline area. Orange scales invade into and partly cover the black margin near dorsal hindwing tornus creating appearance of an orange tooth. Ventral hindwing with broad black or dark brown anal margin. Tuft on hind tibiae long, with dark tip. Orange yellow in color. Peru, Colombia (south), Venezuela (Amazonas), Brazil (north), the Guianas (TL: Suriname).....*P. gentius*
- 3b. Yellow-orange spot in forewing discal cell without hyaline areas. Orange scales do not invade into the black margin near dorsal hindwing tornus, i.e. areas with black scales form close to right angle from the margin to anal fold. Ventral hindwing with fewer black and more yellow-orange scales along anal margin. Tuft on hind tibiae shorter, entirely yellow-orange. Yellower than other species. Peru, Venezuela, Brazil (north, TL: Rondônia), the Guianas.....*P. bombus*



Figure 28. Visual keys to species in the *E. gentius* group. Dorsal and ventral aspects for each species are shown on the left and right, respectively. Images shown are illustrations, sometimes composed of photographic segments from left and right sides and digitally edited to highlight the wing patterns instead of damage in specimens. Images are set to be approximately the same size. Unedited and to scale photographs of specimens are shown in Figs. 1–8. Photographs of all specimens, except *E. huertasae* n. sp. are by Ernst Brockmann.

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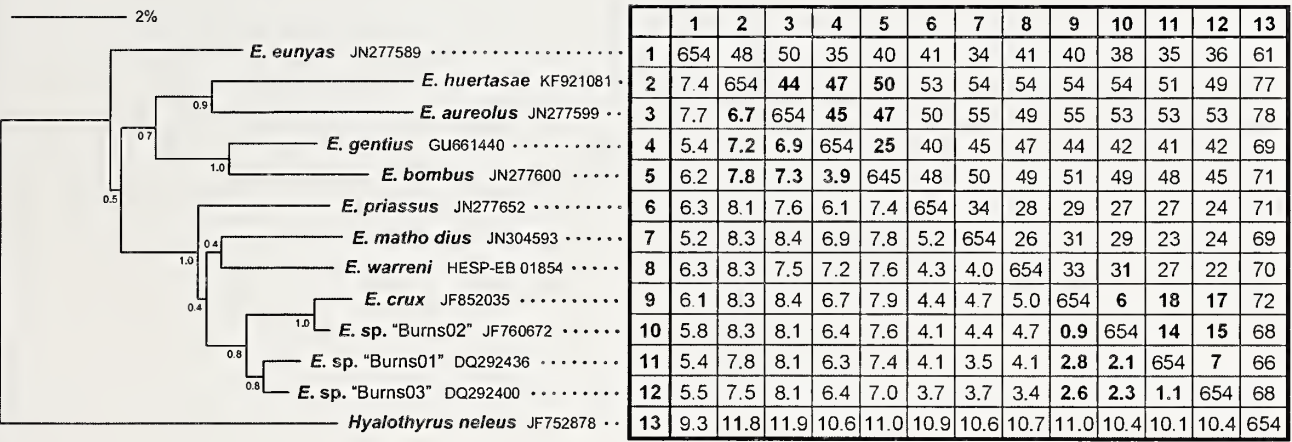


Figure 29. DNA-derived data. The mitochondrial DNA COI barcode (654 base pairs) distance matrix is shown on the right and a BioNJ distance tree (Dereeper *et al.*, 2008) corresponding to it is on the left. The 2% difference scale bar is placed above the tree. Bootstrap support values are shown by each node in the tree. Values below 0.6 correspond to less certain and possibly erroneous groupings. GenBank accessions (<http://genbank.gov>) are indicated to the right of each species name, except that for *E. warreni* sequence, BOLD database (Ratnasingham & Hebert 2007) voucher code is given. The *Entheus* tree was rooted with *Hyalothyrs neleus* (Linnaeus, 1758) sequence. Identification is based on specimen images from the BOLD public web-pages linked to from the “db_xref” fields in the GenBank sequence pages, and should be considered preliminary for some taxa. In the distance matrix, percent difference, the number of different nucleotides and the number of base pairs in a sequence are shown below, above and on the diagonal, respectively. Values corresponding to differences between the four *E. gentius* group species (all specimens from Brazil: Amazonas, except *E. huertasae*, which is from Panama, DNA extraction NVG-1759, full data in text) and four phylogenetically close species in the *E. matho* group are shown in bold. Three of the *E. matho* group species (“Burns01”, “Burns02”, and “Burns03”, sympatric in Costa Rica: Guanacaste Province) remain unnamed, but differences between them have been reported (Janzen *et al.*, 2011).

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